TREE-GRASS AND TREE-TREE INTERACTIONS IN A TEMPERATE SAVANNA

A Dissertation

by

MARK TREVOR SIMMONS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2003

Major Subject: Rangeland Ecology and Management

TREE-GRASS AND TREE-TREE INTERACTIONS IN A TEMPERATE SAVANNA

A Dissertation

by

MARK TREVOR SIMMONS

Submitted to Texas A&M University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Approved as to style and content by:

Steven R. Archer (Co-Chair of Committee)	W. Richard Teague (Co-Chair of Committee)
R. James Ansley (Member)	Michael G. Messina (Member)
Robert E. Whitson (Head of Department)	

August 2003

Major Subject: Rangeland Ecology and Management

ABSTRACT

Tree-Grass and Tree-Tree Interactions in a Temperate Savanna. (August 2003)

Mark Trevor Simmons, B.Sc., University of Lancaster;

B.Sc., University of Cape Town;

B.Sc. (Hons.), University of Cape Town;

M.Sc., University of Cape Town

Co-Chairs of Advisory Committee: Dr. S. R. Archer
Dr. W. R. Teague

Savannas comprise over one eighth of the world's land surface with some 50 Mha in North America alone. They are productive systems supporting a high level of both faunal and floral diversity and are of increasing socioeconomic importance. The maintenance and formation of savannas have been attributed to climate, soils, herbivory and fire. However, the reasons for the coexistence of trees and the grass layer have still to be determined. These two contrasting life forms create a complex of intra- and interspecific positive, negative, and neutral interactions, few of which have been quantified. Under lower-than-average rainfall, tree effects on grasses in a *Prosopis* savanna in northern Texas were largely neutral with few measurable competitive or facultative effects from the tree canopy. However, grasses demonstrated increased productivity where belowground competition with neighboring trees was removed. Similarly, tree growth increased following the removal of grasses under and around individual trees, particularly on shallower soils, but only during a season of significant precipitation. Low intensity burning of grasses enhanced growth of adult trees, but patterns were inconsistent between two different sites. Moderate clipping around individual trees had no apparent effect on tree growth. Intraspecific competition between savanna trees was not evident, but may have been blurred

by an extensive, lateral distribution of near-surface roots. Overall, tree intraspecific competition was neutral regardless of soil depth, suggesting lateral tree roots may be only used opportunistically. Although some competitive relationships were verified, the differences in the responses between the two years of study, and at different sites indicated that soil depth and climate may have overriding impacts on tree-grass interactions and savanna dynamics in this system.

ACKNOWLEDGMENTS

I gratefully thank Dr. Archer for his academic assistance and sustained encouragement throughout my doctoral program. Also my committee co-chair Dr. Teague for his helpful advice and support especially during the field study period. Dr. Ansley similarly provided experimental advice, assistance, and insight into the biology of mesquite. I would like to thank the other members of my graduate committee, Dr. Fisher and Dr. Messina, for their valuable contributions, and Dr. Longnecker for statistical advice.

Several people helped with experimental setup, data collection and laboratory work during this study including: Andy Hubbard, Chris Stokes, Steve Dowhower, Matt Applegath, Jim Nelson, Rebecca Nelson, Chad McMurty, Kye LeBoef, and Deborah Mann-Simmons. Dr. Stuth kindly provided the use of his laboratory, and the staff of the Agricultural Experiment Station, Vernon, Texas provided much practical and logistic assistance.

I gratefully acknowledge the funding for this research provided by a Tom Slick Fellowship, the Heep Foundation, and a Teaching Assistantship provided by the Department of Rangeland Ecology and Management, Texas A&M University.

TABLE OF CONTENTS

Page

ABSTRACT iii

ACKNOWLEDGMENTS v

TABLE OF CONTENTS vi

LIST OF FIGURES viii

LIST OF TABLES xii

CHAPTER

I INTRODUCTION 1

Savannas 1
Tree-grass coexistence 2
Tree effects on grass 3
Grass effects on tree 4
Tree effects on tree 5

II STUDY SITE 8

W. T. Wagonner Estate 8
Climate 9
Pastures 9

III THE INFLUENCE OF HONEY MESQUITE (*PROSOPIS GLANDULOSA*) ON THE GROWTH OF TEXAS WINTERGRASS (*NASELLA LEUCOTRICHA*) AND BUFFALO GRASS (*BUCHLÖE DACTYLOIDES*) IN A TEMPERATE SAVANNA..... 11

Introduction 11
Methods 13
Results 21
Discussion 39

TABLE OF CONTENTS (continued)

CHAPTER		Page
IV	HERBACEOUS UNDERSTOREY EFFECTS ON THE GROWTH OF THE TREE (*PROSOPIS GLANDULOSA*) LAYER IN A TEMPERATE SAVANNA……..	44
	Introduction ……	44
	Methods …….	47
	Results ……...	48
	Discussion …….	59
V	BELOWGROUND INTRASPECIFIC COMPETITION OF HONEY MESQUITE (*PROSOPIS GLANDULOSA*) IN A TEMPERATE SAVANNA …….	65
	Introduction ……	65
	Methods …….	68
	Results ……...	70
	Discussion …….	82
VI	SUMMARY AND CONCLUSIONS ……. ……..……	85
	Tree on grass effect… ……	85
	Grass on tree effect …….	86
	Tree on tree effect ……	87
	Directions for future research …….	88
REFERENCES ……..….		89
APPENDIX ……		102
VITA ……..……		118

LIST OF FIGURES

FIGURE		Page
1	Rainfall patterns during 1998 (solid) and 1999 (hatched) at deep (A) and shallow (B) soil sites. Line represents local 30-year monthly mean……	10
2	Diagrammatic representation of experimental treatments that isolated above- and belowground competition between individual *P. glandulosa* trees and the adjacent herbaceous layer…….	15
3	Diagrammatic representation of experimental treatments that isolated above- and belowground competition between individual *P. glandulosa* trees and the adjacent herbaceous layer in midgrass sites. The '*' indicates synthetic shade treatment consisting of acetate film and neutral density shade cloth. Dashed tree outline indicates where a tree was removed. Small vertical bars below soil surface indicate root barriers. Treatments A through F were located in the subcanopy and G through J in interstitial locations. Treatments A and G represent natural conditions…….	16
4	Spectral fluence rate response to shade screen and acetate ambient light modification. Ambient R:FR ambient ratio 1.09; *P. glandulosa* R:FR ratio: 8.49; acetate R:FR ratio: 0.710……	18
5	Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and relative basal area growth per plant (from start to end of the growing season), tiller density, and reproductive tiller density, response to competitive treatments for midgrass sites in 1998 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition)……..	22
6	Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and relative basal area growth per plant (from start to end of the growing season), tiller density, and reproductive tiller density, response to competitive treatments for midgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition)……..	25

LIST OF FIGURES (continued)

FIGURE Page

7 ANPP estimated from dry-weight rank method of herbaceous groups response to competition treatments in 1999 (see Fig. 2 for treatment labels). Bars with different letters indicate significant difference at P < 0.05. Dotted line separates subcanopy from interstitial sites…… 26

8 Mean (± SE, n = 8) herbaceous ANPP in the presence and absence of above- and belowground competition for subcanopy and interstitial midgrass sites during 1999. Panel titles denote data pooling corresponding to statistical contrasts. Bars with different symbols are different at the P < 0.05 level……. 33

9 Mean (± SE, n = 8) of *N. leucotricha* reproductive tiller density in the presence and absence of above- and belowground competition for subcanopy and interstitial midgrass sites during 1999. Panel titles denote data pooling corresponding to statistical contrasts. Bars with different symbols are different at the P < 0.05 level……..…… 34

10 Herbaceous ANPP, *B. dactyloides* plant density, relative tiller production, tiller density, and reproductive tiller density, response to competitive treatments for shortgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition)……. 35

11 Mean (± SE, n = 8) shortgrass plot herbaceous ANPP in the presence aboveground competition for subcanopy and interstitial shortgrass sites during 1998. Bars with different symbols are different at the P < 0.10 level…… 36

12 Herbaceous ANPP, *B. dactyloides* plant density, relative tiller production, tiller density, and reproductive tiller density, response to competitive treatments for shortgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition)……. 37

13 Mean (± SE, n = 8) *B. dactyloides* tiller density for subcanopy and interstitial during 1999. Bars with different symbols are different at the P < 0.10 level…… 38

LIST OF FIGURES (continued)

FIGURE Page

14 Mean (± SE; n = 5) relative basal area growth of *P. glandulosa* trunks in response to understory manipulation (control= no treatment, mowed, remove = herbicided, and burned) during 1998 (solid bar) and 1999 (hatched bar) on sites with contrasting soil depths. Results of repeated measures ANOVA shown for each site. For a given site, bars with different letters were significantly different at P ≤ 0.05…… 53

15 Patterns of mean (± SE; n = 5) soil moisture (neutron scattering; volumetric) with depth on control plots (herbaceous layer intact; closed circles) and herbaceous removal plots (open triangles) on deep (A) and shallow (B) soils during the 1999 growing season. Asterisks indicate significant differences (P ≤ 0.05) between control and removal moisture profiles. Readings were made 4 meters horizontally from *P. glandulosa* stem. …… 57

16 Mean (± SE; n = 5) surface (30 cm) soil moisture (TDR; volumetric) at 1m, 2m, and 4m meters from *P. glandulosa* stems in 1999 on deep (A) and shallow (B) soil plots where the herbaceous layer was intact (control; solid circles) or removed (open triangles). Arrow represents average location of tree canopy drip-line……..……. 58

17 Mean (± SE; n = 5) leaf N (A) and P (B) (% dry weight) of *P. glandulosa* plants in July 1999 in response to understory manipulation (control = intact; mown, remove = herbicided, burned) with contrasting soil depths. Bars with different letters denote significant differences at P ≤ 0.05. Absence of letters denotes no significant difference between bars……. 60

18 Relationship between mean (± S.E.) of relative annual basal growth of *P. glandulosa* plants with (standing) and without neighbors (cleared)……. 73

19 Relationship of mean (± S.E.) length of terminal shoots (cm) of individual *P. glandulosa* plants to soil depth and presence (standing) and absence (cleared) of neighbors during 1999…….. 77

LIST OF FIGURES (continued)

FIGURE Page

20 Relative basal growth of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on deep soil sites at end of 1998 and 1999 season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand..……. 78

21 Relative basal growth of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on shallow soil sites at end of 1998 and 1999 season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand…….. 79

22 Length of terminal shoots (cm) of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on deep (A, C) and shallow (B, D) soil sites at end of 1999 growing season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand……. 80

23 Response of individual *P. glandulosa* canopies to herbicide injection at points along 1 m perpendicular lines (+). Circles represent locations of *P. glandulosa* canopies in relation to '+' (to scale). Empty circle = no canopy effect; gray fill = 0-33% canopy dieback; hatched fill = 34-66% dieback; solid fill = 67-100% canopy dieback. Dotted line circumscribes area within 15-m of '+'. 81

LIST OF TABLES

TABLE		Page
1	Factorial design of the experiment examining the influence of *P. glandulosa* on the herbaceous layer beneath (subcanopy) and away (interstitial) from tree canopies showing presence (+) or absence (-) of above- and belowground competition/facilitation settings within experimental layout…….	14
2	Summary of tested multiple contrasts for tree-grass competition treatments used to test hypotheses, and contrast direction for each growth parameter for hypothesis (H) to hold. Positive (+) and negative (-) sign refers to presence or absence of competition. Gap = interstitial site; Sub = subcanopy site……..	19
3	Multiple contrasts for 1998 mid-grass plot ANPP, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526), ** (P < 0.05 with Bonferroni correction P < 0.00263), and *** (P < 0.01 with Bonferroni correction P < 0.00053)……..	23
4	Multiple contrasts for 1998 *N. leucotricha* shoot biomass ($g \cdot m^{-2}$), tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < .00053)..……	24
5	Summary of ANOVA results of ANPP (dry-rank weight method) for site (subcanopy vs. interstitial) and functional group (*N. leucotricha*, annual grasses, forbs) main effects and interactions in 1999……	28
6	Multiple contrasts for 1999 mid-grass ANPP tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053)……. ……..	29

LIST OF TABLES (continued)

TABLE		Page
7	Multiple contrasts for 1999 *N. leucotricha* reproductive tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053)…….	30
8	Multiple contrasts for 1998 short-grass ANPP, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by *(P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011)…….	31
9	Multiple contrasts for 1999 *B. dactyloides* tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011)…….……..	32
10	Means and standard errors of initial stem basal area and absolute annual growth rate of *P. glandulosa* trees at shallow, intermediate, and deep soil sites. Means with different letters indicate differences at P < 0.01…….	49
11	Summary of regression results for the relationship between absolute annual growth rate ($cm^2 \cdot cm^{-2} \cdot yr^{-1}$) and initial basal area (cm^2) of *P. glandulosa* for soil depth (shallow, intermediate m and deep) and year (1998, 1999)…….	50
12	Summary of independent repeated measures ANOVA results for each soil depth for year (1998, 1999), and herbaceous manipulation treatment (control, mow, sward removal, burn) main effects and interactions on basal area growth of *P. glandulosa*……	52

LIST OF TABLES (continued)

TABLE		Page
13	Summary of repeated measures ANOVA results for site (shallow vs. deep soil), depth in soil profile (depth, 0-115 cm), date (month of year in 1999), and treatment (control, sward removal) main effects and interactions on soil moisture profiles during 1999……	54
14	Summary of repeated measures ANOVA results for site (shallow vs. deep), treatment (control, mow, sward removal), distance from tree bole (1, 2, 4 m), and date (month of year, 1999) main effects and interactions on TDR measured surface soil moisture during 1999……..	55
15	Summary of ANOVA results for site (shallow, intermediate and deep soil), treatment (control, mow, sward removal) main effects and interactions on leaf N and P measured in 1999……..	56
16	Regression model statistics assessing the relationship of absolute stem growth with initial stem basal area at deep and shallow soils…….……..	71
17	Repeated-measures ANOVA model statistics assessing effects of soil depth (deep vs. shallow), presence or absence of neighbors (±) and their interaction on relative, annual basal growth of *P. glandulosa* target trees after the 1998 and 1999 growing season…….	72
18	ANOVA model statistics assessing effects of soil depth (deep vs. shallow), presence or absence of neighbors (±) and their interaction on the stem length of *P. glandulosa* target trees after the 1999 growing season…….	75
19	Summary of ANOVA model statistics for the measures of effect ground- injected herbicide on neighboring *P. glandulosa* trees within 15 m…….	76

CHAPTER I

INTRODUCTION

SAVANNAS

Savannas can be defined as ecosystems with a discontinuous woody component overlying a continuous herbaceous layer. They comprise over one eighth of the Earth's surface, occupying some 50 MHa in North America alone (McPherson 1997). Grassland and savanna systems support high faunal and floral diversity, and are of increasing socioeconomic importance (Young and Solbrig 1993). The existence of savannas has been attributed to a number of interactive determinants including climate (rainfall amount and seasonality), soils (depth and fertility), herbivory (balance between grazing and browsing) and fire (Walker and Noy-Meir 1982, Skarpe 1992, Jeltsch et al. 1996, Scholes and Archer 1997). Throughout the past century, the encroachment of unpalatable woody species, attributed to changes in climate, grazing, and fire regimes (Madany and West 1983, Archer et al. 1988) has become a major problem for land managers (McPherson et al. 1988, Grover and Musick 1990, Archer 1994, Archer et al. 2001). The co-occurrence of these contrasting plant lifeforms creates a complex of both intra- and interspecific interactions, many of which have yet to be quantitatively studied, and has thus invited more applied research to understand savanna interactions. This study examines the interactions between the two major plant components of savannas so that management techniques can more effectively manipulate the balance between trees and grasses to achieve land use goals.

This dissertation follows the style and format of Ecology.

TREE-GRASS COEXISTENCE

The principal reasons for coexistence in savannas have still to be determined (Jeltsch et al. 1996). Disequilibrium models propose that coexistence occurs where the effect of environmental changes, such as fluctuations in climate, ecological disturbances (Walker and Noy-Meir 1982, Yeaton 1988) or herbivory (Walker and Noy-Meir 1982), are more significant than interspecific competition (Scholes and Archer 1997, Higgins et al. 2000). Alternatively, simple models of belowground resource acquisition have suggested that resource partitioning perpetuates coexistence of these two growth forms, whereby deep-rooted trees access water from layers deeper in the soil profile than shallow rooted grasses (Walter 1971, Weltzin and McPherson 1997) (but see Knoop and Walker 1985). Similarly, if we assume that trees can produce deeper roots, we can envisage that a bimodal rainfall pattern may temporally partition this resource on deep soils. Rainfall during the winter, while grasses are dormant, recharging the lower portion of the soil profile would favor tree growth; alternatively, grass production would be supported by summer rain events (Walter 1971, Walker and Noy-Meir 1982, Knoop and Walker 1985, Ehleringer et al. 1991). This further suggests that edaphic characteristics may have a significant influence on the relative competitive abilities of trees and grasses, and changes in both individual species characteristics (Pelaez et al. 1994) and soil texture and depth (e.g. Johnson and Tothill 1985, Knoop and Walker 1985, Archer 1995b, Barnes and Archer 1999) may directly affect the grass-woody plant ratio. However, if both life forms are synchronously active and occupy coincident space, then both above- and belowground competition may have an additional influence on tree-grass coexistence (Ehleringer et al. 1991). Trees may, for example, ameliorate the sub-canopy environment, potentially promoting understorey establishment and production, but nevertheless actively compete for resources with these same plants (Belsky 1994, Barnes and Archer 1999).

The encroachment of honey mesquite (*Prosopis glandulosa* Torr.) in the Rolling Plains of northern Texas, due to fire suppression, reduction of grass competition, and increased seed dispersal from cattle, has been widespread across different soil types and herbaceous plant species communities (Fisher 1950, McDaniel et al. 1982, Archer 1995b, Ansley and Jacoby 1998). This has resulted in the formation of a relatively young savanna system largely dominated by one species of tree. However, we know little of the mechanics of this system. Hence, the goal of this study is to identify the main tree-grass interactions that govern vegetation dynamics of temperate savannas in this region by experimentally assessing tree effects on grasses, grass effects on trees, and tree effect on trees.

TREE EFFECTS ON GRASS

The vast majority of savanna research has emphasized woody plant effects on the herbaceous layer. This has shown that the effects of woody plants on grasses can range from positive to neutral to negative, the outcomes of these interactions varying depending on component plant physiology, climate patterns, herbivory, soil, and fire (Archer 1995b, Scholes and Archer 1997). Existing research on *P. glandulosa* has suggested both negative (Dahl et al. 1978, McDaniel et al. 1982, Bedunah and Sosebee 1986, Heitschmidt and Dowhower 1991, Laxson et al. 1997) and neutral (Heitschmidt et al. 1986) tree-grass effects. Studies in tropical and sub-tropical systems have shown where tree densities are low, herbaceous productivity under or near tree canopies can be greater than open areas (Belsky 1994). However, as tree densities increase, herbaceous production typically declines (e.g., McPherson 1992). The nature of the tree-grass interaction will depend on canopy and rooting characteristics of woody plants, rainfall, soil properties, and disturbance regime. Belsky and Canham (1994) attributed the differences in productivity between open-grassland and below-canopy sites to three primary factors:

1. Improved fertility and structure of soils below tree crowns
2. Improved water relations of shaded plants
3. Competition between trees and understorey plants for soil moisture and nutrients

There is conflicting evidence for the beneficial effects of the presence of both tree canopies and roots on the water balance and nutrient uptake and abiotic conditions experienced by plants growing beneath the canopy or within the influence of the rooting zone. Trees can have both an above- and belowground effect which may improve or reduce water status (Tiedemann and Klemmedson 1977, Heitschmidt et al. 1988, Ansley et al. 1991, Dawson 1993, Belsky 1994), increase nutrient concentration (Fisher 1990, Scholes and Archer 1997, Amiotti et al. 2000, Isichei and Muoghalu 1992), alter soil physical characteristics, (Tiedemann and Klemmedson 1973, Fisher 1995) and subcanopy climate (Smith 1975, Lee 1985, Haworth and McPherson 1995).

GRASS EFFECTS ON TREE

Although numerous studies have examined the effect of trees on grasses, few have looked at the effect grasses might have on adult trees (Scholes and Archer 1997). There are some indications that a healthy herbaceous layer should compete with woody plants for resources and repress woody growth (Scifres et al. 1974, Scifres and Polk 1974). Although woody seedling growth may be repressed by the herbaceous layer (Archer 1995a, McPherson 1997), effects on mature trees range from neutral (McPherson and Wright 1989) to strongly negative (Stuart-Hill and Tainton 1989). It has been demonstrated that *P. glandulosa* can be dependent on shallow lateral roots (Ansley et al. 1991) suggesting that the grass layer may affect tree growth where roots of both growth forms are coincident. Studies from southern Africa suggest that grass-tree influences may be a function of soil type. The ability of the herbaceous layer

to compete with trees for water may be reduced on coarse-textured soils where water can percolate deeper through the soil profile to which trees have exclusive use (Knoop and Walker 1985). However, grazing, by reducing above- and belowground biomass, may neutralize the competitive suppression of tree growth by grasses (Stuart-Hill and Tainton 1989).

Fire has been an important determinant of woody plant abundance in many savannas (Jensen et al. 2001). Increased fire frequency in many systems may be altering savanna relations by directly affecting species composition and indirectly affecting soil nutrients (Dumontet et al. 1996, Jensen et al. 2001). The role of fire in maintenance of savannas ranges from one of complete mortality of woody plants, to one of modifying structure of savannas dominated by fire-tolerant woody species (Scholes and Walker 1993). Consequently, most savanna research regarding the effect of fire on woody plants has examined seedling mortality and vegetative regeneration of established adult trees. However, individuals of larger stature often escape with minimal canopy damage (Scholes and Walker 1993) and post-fire competitive and soil characteristics many enhance surviving tree growth. Fire is known to enhance post-fire woody seedling establishment by increasing available nitrogen, phosphorus, potassium, calcium, and magnesium in the mineral soil (Christensen 1977, McKee 1982, Covington and Sackett 1984, Schoch and Binkley 1986, Jensen et al. 2001). Consequently, it has been proposed that low intensity understorey fires will similarly stimulate growth in fire-resistant adult trees (de Ronde et al. 1990). However, it is difficult to predict the importance of this mechanism in maintenance of savannas and this hypothesis has yet to be tested.

TREE EFFECTS ON TREE

Although intraspecific competition among even-aged woody plants (Kenkel 1988, Baldwin et al. 2000) and woody saplings (Shainsky and Radosevich 1992) has been demonstrated, evidence for the importance of such interactions in natural woodlands (Duncan 1991), and savannas (Scholes and

Archer 1997) is sparse and indirect. With relatively lower woody stem densities, intraspecific competition in savannas has received less attention than the interaction between the woody and herbaceous components. As tree densities increase during the course of woody encroachment, it can be envisaged that the effects of intraspecific competition and density dependent effects on growth and mortality would become progressively more important (e.g., Van Auken and Bush 1987).

Evidence of competition between savanna trees has been largely inferential (Penridge and Walker 1986, Kenkel 1988, Martens et al. 1997, Scholes and Archer 1997), but has indicated that competition intensity increases with increasing tree density. Tree distribution in savannas can be an indicator of both inter- and intraspecific competition (Martens et al. 1997). Removal experiments in shrublands have shown that intraspecific competition may or may not occur, depending on resource availability and rooting patterns (Manning and Barbour 1988, McPherson and Wright 1989). Experimental manipulations have demonstrated that trees may benefit from the removal of conspecific neighbors (Ford 1975) and greenhouse experiments on *P. glandulosa* seedlings have demonstrated marked density effects on leaf number, stem length, basal diameter, and biomass (Van Auken and Bush 1987). The characteristics of the soil environment may also influence tree-tree competitive interactions. Research in north Texas savannas has demonstrated that *P. glandulosa* trees may rely heavily on lateral roots, particularly where availability to subsurface water is reduced (Ansley et al. 1990, Ansley et al. 1991, Ansley et al. 1992a, Cuomo et al. 1992). Allocation of resources to near-surface, lateral roots therefore increase the probability of competitive interactions with other individuals which themselves may be displaying similar rooting characteristics. (Van Auken and Bush 1987). In a stand removal field experiment Ansley et al. (1998) demonstrated evidence for density dependent growth characteristics in adult *P. glandulosa* in contrasting stand densities.

The goal of this dissertation is to quantify interactions between trees and grasses in the *P. glandulosa* savanna of north Texas, and differentiate these effects from site-specific influences such as soil depth. To describe the relative importance of above- and belowground competition, Chapter III examines the effect of *P. glandulosa* on the underlying herbaceous layer through a suite of experimental manipulations of the tree canopy and tree roots in both subcanopy sites and the areas between trees. Chapter IV studies the reverse role: the effect of the herbaceous layer on tree growth using burning, mowing, and removal of the understorey herbaceous layer on sites of contrasting soil depth. Finally, in Chapter V the intraspecific interaction between individuals of *P. glandulosa* are examined through the observation of the growth response following removal of neighborhood trees across a range of stand densities and on both shallow and deep soils.

CHAPTER II

STUDY SITE

W.T. WAGGONER ESTATE

Experiments were conducted on the W.T. Waggoner Estate (Clayton 1993), Wilbarger County, near Vernon, Texas (34º 08' N, 99º 18' W; elevation 381 m; mean annual rainfall 665 mm). Landscapes at the study site consisted of gently rolling hills (10–20 m elevation changes) with varying densities of *P. glandulosa* individuals. Historically a grass-dominated landscape (Teague et al. 1997), the north Texas Rolling Plains have been extensively invaded by *P. glandulosa* (Teague et al. 1997) since the early 1900s (Asner et al. 2003). Ranch pastures received extensive brush clearing up to the 1980's using a variety of chemical and mechanical techniques (Ansley et al. 1995, Asner et al. 2003). *P. glandulosa* is now the dominant woody species, at densities ranging from 0 - 500 trees·ha^{-1} (Ansley et al. 1995) depending on management history. The herbaceous matrix consists of C_3 (e.g. annual *Bromus* spp. and perennial *Nassella leucotricha*) and C_4 (e.g. perennial *Buchlöe dactyloides*, *Bouteloua curtipendula*) grasses. In heavily grazed, 'lawn' areas the C_4 shortgrass *B. dactyloides* tends to dominate, with *N. leucotricha* and C_4 midgrasses in lightly grazed areas (Teague and Dowhower 2002). The Waggoner Ranch has generally experienced moderate cattle grazing with stocking rates of ca. 11 - 12 ha·head^{-1} over the last 20 years, and about 8 ha·head^{-1} prior to this (Teague et al. 1997). The clay-loam flats range sites consist of moderately deep clay-loams of the Tilman series (fine, mixed, thermic Typic Paleustoll) with 1 to 3% slopes overlying sandstone and shale (USDA 1962, Daigal 1978). The shallow-clay range sites consist of moderately fertile shallow-clays of the Vernon series (fine, mixed, active, thermic Typic Haplustepts) with 3 to 8% slopes.

CLIMATE

The Rolling Plains region of north central Texas experiences a subtropical, subhumid climate, characterized by hot summers and dry winters (Larkin and Bomar 1983). Vernon, Texas has a mean annual temperature of 17°C with 30 days·y^{-1} of >38°C. Mean monthly high temperature is 29°C in July; the mean monthly low is 4°C in January (Bomar 1983, NOAA 2001). Annual rainfall is bimodally distributed with peaks in May (104 mm) and September (89 mm) (National Oceanic and Atmospheric Administration 2001). The year prior to study (1997) was wetter than the long-term average whereas the years of the study (1998 and 1999) were significantly below average, especially during the growing season (Fig. 1) (Texas Water Development Board 2002). Rainfall recorded at the deep and shallow soil sites in 1998 was lower than that received in 1999 (665 mm) (Fig. 1). Monthly rainfall patterns were also slightly different between sites. In 1998 the shallow soil site received slightly less rainfall than the deep soil site, with no measurable rainfall from July through September. Conversely, the shallow soil site received more rainfall than the deep soil site in spring and late summer in 1999 (Fig. 1).

PASTURES

Experiments were conducted in level, upland landscape elements selected for differences in variation of depth to underlying parent material. The Hazelwood Pasture 'shallow' site (33º 57' N, 99º 04' W, elev. 360 m) had a soil depth of 1.0-1.2 m. Soils in the Four-Corners Pasture (33º 54' N, 99º 20' W, elev. 370 m), had a depth of 2-3 m, and those in the Nine-mile Pasture 'deep' site (33º 51' N, 99º 26' W, elev. 381 m) had a depth of 3-4 m. These pastures are located along a 33-km line running approximately east-northeast to west-southwest. The Hazelwood and Four corners Pastures are 32 km and 9 km east-northeast of Nine-mile Pasture respectively. Rain gauges were installed at the Nine-mile and Hazelwood sites.

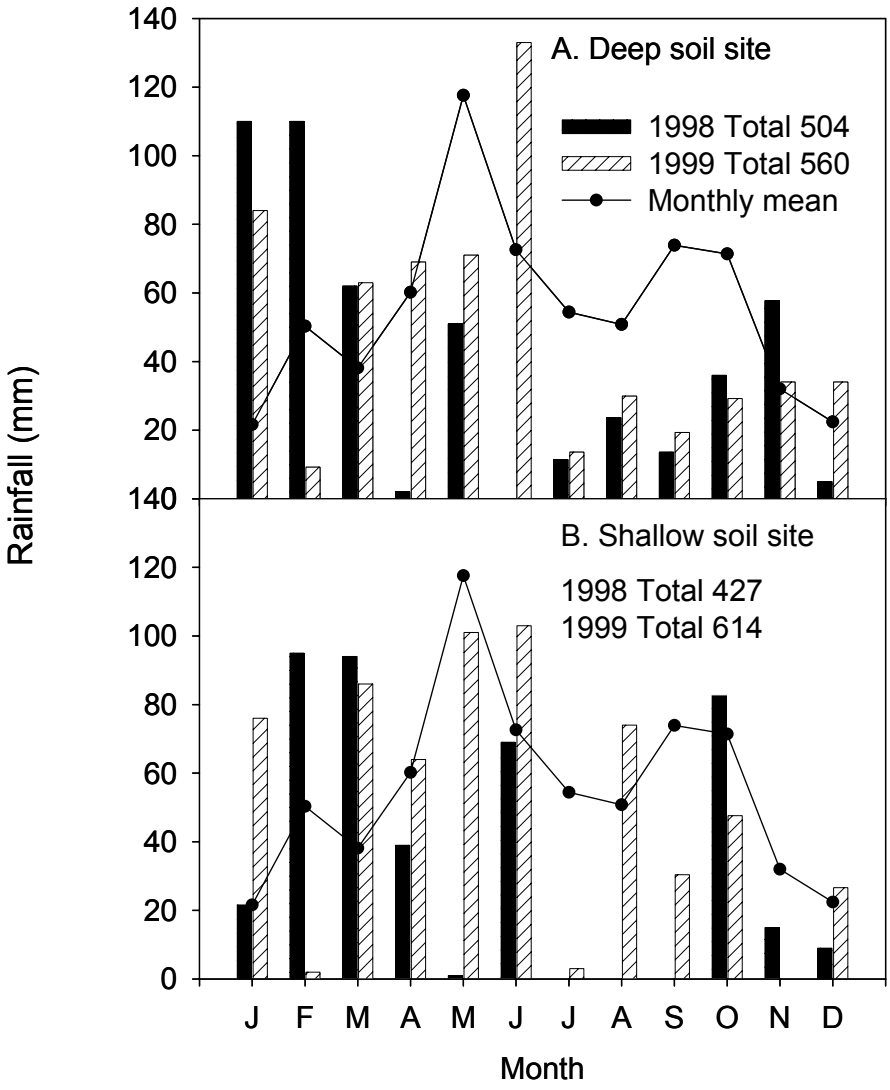

Fig. 1. Rainfall patterns during 1998 (solid) and 1999 (hatched) at deep (A) and shallow (B) soil sites. Line represents local 30-year monthly mean.

CHAPTER III

THE INFLUENCE OF HONEY MESQUITE (*PROSOPIS GLANDULOSA*) ON THE GRWOTH OF TEXAS WINTERGRASS (*NASSELLA LEUCOTRICHA*) AND BUFFALO GRASS (*BUCHLÖE DACTYLOIDES*) IN A TEMPERATE SAVANNA

INTRODUCTION

Savanna trees can impose both above- and belowground effects on the subcanopy environment, altering water status, nutrients, and microclimate. These modifications may have positive, neutral, or negative effects on the production of herbaceous vegetation beneath tree canopies (Scholes and Archer 1997). Few studies have attempted to differentiate between the effects or relative importance of the separate, although not necessarily mutually exclusive factors (Scholes and Archer 1997, Archer et al. 2001). There are many proposed mechanisms governing tree-grass interactions but these are variable and frequently interactive. Belsky and Canham (1994) attributed the differences in productivity between open-grassland and below canopy sites to three primary interacting and potentially off-setting or reinforcing factors:

1. Improved fertility and structure of soils below tree crowns
2. Improved water relations of shaded plants
3. Competition between trees and understory plants for light, soil moisture and nutrients

In tropical and sub-tropical systems, where tree densities are low, herbaceous productivity under or near tree canopies has been shown to be greater than that in inter-canopy areas (see Belsky 1994). In these cases, benefits associated with soil nutrient enrichment (Fisher 1990, Isichei and Moughalu 1992, Mordelet et al. 1993), and temperature amelioration appear to outweigh reductions in

photosynthetically active radiation and rainfall interception by tree canopies. Alternatively, sub-canopy grass growth may be reduced by the presence of tree-canopies suggesting that deleterious effects associated with decreases, in available light, and/or canopy interception of rainfall (McPherson 1997, Scholes and Archer 1997) outweigh positive effects. Although there is evidence for belowground resource partitioning in several savannas (Soriano et al. 1983, Knoop and Walker 1985) and in *P. glandulosa* savanna in Texas (Brown and Archer 1990), there is contrary evidence that, near-surface tree roots may actively compete with grasses for resources depending on water availability (Belsky 1994, Breshears et al. 1997).

We know little of the mechanics of tree-grass interactions in the mesquite temperate savannas of northern Texas. Existing studies suggest *P. glandulosa* may have negative (Dahl et al. 1978, McDaniel et al. 1982, Heitschmidt and Dowhower 1991, Laxson et al. 1997) or neutral (Heitschmidt et al. 1986) effects on herbaceous production. Evidence from huisache (*Acacia farnesiana*) savannas in south Texas indicated that at the landscape scale there may be both positive and negative tree canopy effects resulting in maximum grass production at an intermediate canopy cover of approximately 25% (Scifres et al. 1982). The extensive lateral root architecture of *P. glandulosa* (Fisher 1950, Tiedemann and Klemmedson 1977, Heitschmidt et al. 1988, Ansley et al. 1991) suggests that *P. glandulosa* may also affect herbaceous production of inter-canopy zones. The objective of this study was to determine (a) if production of the subcanopy herbaceous layer would be comparable to, greater than, or less than that in interstitial zones, (b) whether differences in subcanopy vs. interstitial production (if any) were due to the modification of the aboveground (light and temperature) or belowground (water and nutrients) environment, (c) if there was any difference in the response of the C_3 (*Nassella leucotricha*) versus C_4 (*Buchlöe dactyloides*) grass components; and (d) if *P. glandulosa* competitive

effects extend beyond its canopy. These objectives were addressed using elective removal and exclusion experiments to test the following hypotheses:

H1 - Sub-canopy and interstitial grass growth will increase following removal of belowground competition with trees (Belsky 1994).

H2 - Sub-canopy grass growth will be enhanced relative to that of interstitial zones, due to fertile-island effect (Mordelet et al. 1993), but only if radiant energy is attenuated.

H3 - Sub-canopy grass growth will be enhanced by the presence of the tree-canopy (Heitschmidt et al. 1986), but only if soil nutrients are enriched.

H4 - Removal of the canopy and subsequent alteration of the light/temperature environment will differentially affect the growth of *B. dactyloides* (C_4) and *N. leucotricha* (C_3) (Heitschmidt et al 1986).

METHODS

Experiment 1

A randomized-block experiment was established to separate the mechanisms contributing to the net outcome of facilitative vs. competitive interactions between *P. glandulosa* and *N. leucotricha*. Ten treatments were applied to herbaceous 'midgrass' (dominated by *N. leucotricha*) plots (0.25 m^2) situated under (subcanopy) and away (interstitial) from *P. glandulosa* tree canopies, creating different combinations of below- and aboveground competition (n = 8 per treatment; Table 1; Fig. 2 & 3). The treatments were installed in the Hazelwood pasture (see Chapter II) in December 1997; data readings commenced 1998. For treatments minimizing *P. glandulosa* root competition, vertical trenches were excavated with a gasoline-powered trencher

Table 1. Factorial design of the experiment examining the influence of *P. glandulosa* on the herbaceous layer beneath (subcanopy) and away (interstitial) from tree canopies showing presence (+) or absence (-) of above- and belowground competition/facilitation settings within experimental layout.

Subcanopy		Interstitial	
above	below	Above	below
+	+	n/a	n/a
+	-	n/a	n/a
-	+	-	+
-	-	-	-
+ (synthetic)	+	+ (synthetic)	+
+ (synthetic)	-	+ (synthetic)	-

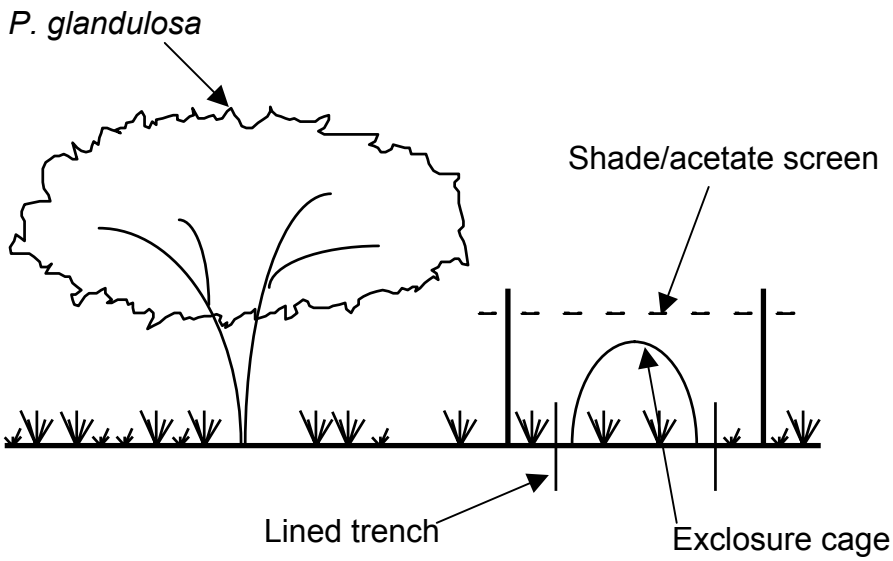

Fig. 2. Diagrammatic representation of experimental treatments that isolated above- and belowground competition between individual *P. glandulosa* trees and the adjacent herbaceous layer.

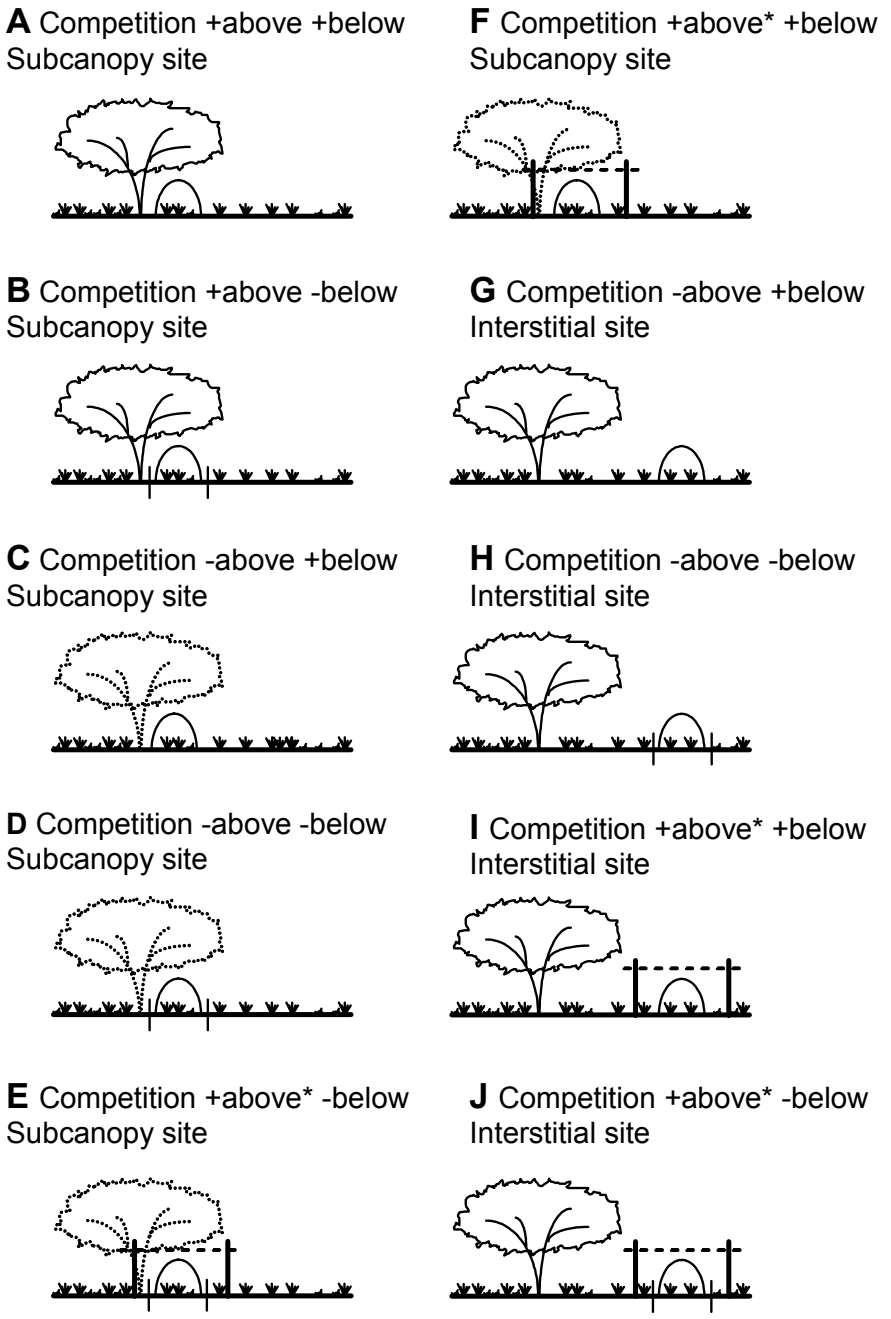

Fig. 3. Diagrammatic representation of experimental treatments that isolated above- and belowground competition between individual *P. glandulosa* trees and the adjacent herbaceous layer in midgrass sites. The '*' indicates synthetic shade treatment consisting of acetate film and neutral density shade cloth. Dashed tree outline indicates where a tree was removed. Small vertical bars below soil surface indicate root barriers. Treatments A through F were located in the subcanopy and G through J in interstitial locations. Treatments A and G represent natural conditions.

(Case 460) to a depth of 1 m, lined with 6-mil black polythene, then backfilled. Care was taken to avoid disturbing the soil hydrological environment by placing root barriers ca. 1 m from the plot perimeter. For treatments seeking to differentiate between *P. glandulosa* canopy effects and soil nutrient effects, trees were cut at ground level and removed, and replaced with artificial shade structures designed to mimic the *P. glandulosa* radiant energy regime. Where trees were felled to remove the aboveground competitive component, stumps were allowed to resprout minimizing root dieback without shading the herbaceous target area. Spectroradiometer (Li-COR LI-1800) measurements indicated mid-day R:FR ratio of 0.849 (± 0.171) beneath *P. glandulosa* canopies (n = 3; Fig. 4). These radiant energy regimes were approximated on the *P. glandulosa*-modified soil patches using 'simulated canopies' similar to that suggested by Lee (1985), consisting of colored acetate (Roscolox 66 "cool blue") sandwiched between neutral-density window screen (1 mm x 1 mm) cloth and a structural wire mesh. R:FR beneath simulated canopies was 0.708 (± 0.003). Identical shade structures were placed in interstitial zones to create *P. glandulosa*-like changes in the radiant energy regime on *N. leucotricha*-dominated patches occurring on soils that had not been modified by the presence of a tree. The artificial *P. glandulosa* canopies were orientated east-west and tilted at an angle of approximately 25 degrees from the horizontal, dipping toward the south, such that there was maximum shade exposure to the target area below, while allowing the circulation of air and penetration of un-modified early morning and late afternoon sun (as occurs with an actual *P. glandulosa* canopy). The passage of rainfall was enabled by perforating the acetate with a grid of 1 cm holes 2.5 cm apart. This perforation also served to create some radiation 'dappling' that occurs in real canopies. For the second year of study, permeability of this structure to rainfall was improved by cutting the acetate with parallel slits 5-10 cm apart.

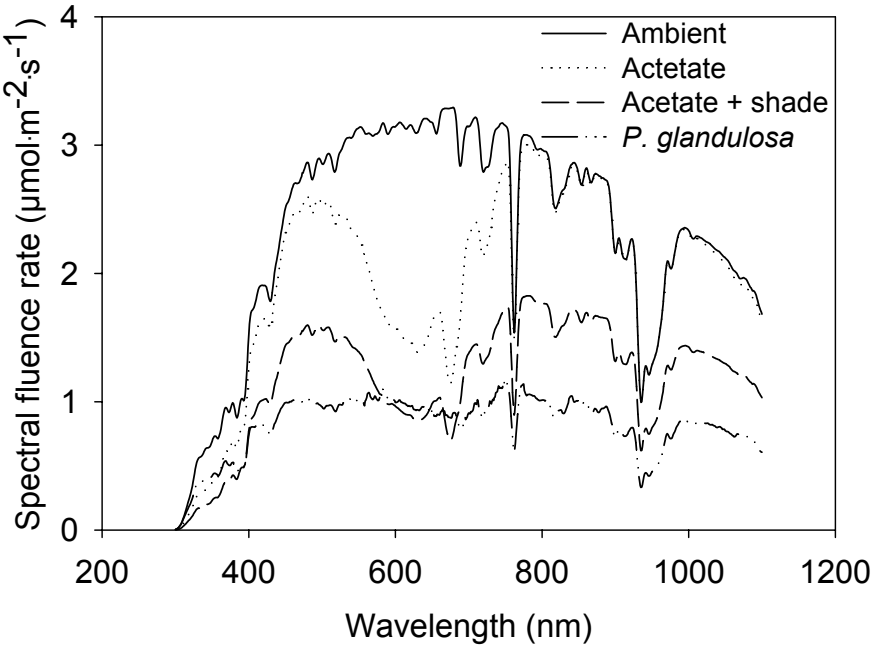

Fig. 4. Spectral fluence rate response to shade screen and acetate ambient light modification. Ambient R:FR ratio 1.09; *P. glandulosa* shade R:FR ratio: 0.849; acetate R:FR ratio: 0.710.

Table 2. Summary of tested multiple contrasts for tree-grass competition treatments used to test hypotheses, and contrast direction for each growth parameter for hypothesis (H) to hold. Positive (+) and negative (-) sign refers to presence or absence of competition. Gap = interstitial site; Sub = subcanopy site.

	Contrast description and contrast direction (<, >)	**Hypotheses tested**
1	subcanopy > gap	Hypothesis 2
2	+above > -above	Hypothesis 3
3	+below < -below	Hypothesis 1
4	+above +below < (H1) > (H3) -above -below	Hypotheses 1 & 3
5	+above +below > -above +below	Hypothesis 3
6	+above -below > -above -below	Hypothesis 3
7	sub +below < -below	Hypothesis 1
8	sub +above > -above	Hypothesis 3
9	sub +above +below < (H1) > (H3) -above -below	Hypotheses 1 & 3
10	gap -below > +below	Hypothesis 1
11	gap +above > -above	Hypothesis 3
12	gap +above +below < (H1) > (H3) -above -below	Hypotheses 1 & 3
13	sub -below > gap -below	Hypothesis 1
14	sub +below > gap +below	Hypothesis 2
15	sub -above > gap -above	Hypotheses 2
16	sub +above > gap +above	Hypotheses 2
17	natural shade = synthetic shade	Tests shade type
18	natural shade > no shade	Hypothesis 3
19	synthetic shade > no shade	Hypothesis 3

Measurements of *N. leucotricha* growth included relative change of tillers per plant (%) and basal area (%) from beginning to end of the growing season, and reproductive and non-reproductive tiller density (tillers·cm^{-2}), and aboveground net primary production (ANPP; g·m^{-2}) of all herbaceous species and *N. leucotricha* at the end of each growing season (1998, 1999). Although this experiment was balanced (equal sample sizes), it was impossible to install some experimental combinations (e.g. a natural canopy shade (tree) in an interstitial site), and consequently the factorial experimental layout had missing 'cells'. Statistical analyses therefore, examined contrasts between different treatments within a general linear model using SAS (SAS Institute Inc. 1988) with Bonferroni correction (Keppel 1991) applied to each comparison. Table 2 shows a summary of contrasts tested and conditions necessary to support the stated hypotheses.

Coarse compositional data were recorded and biomass quantified using the dry-weight-rank method (Sandland et al. 1982), grouping the herbaceous plant species into the following functional groups: *N. leucotricha;* annual grasses (mainly *Bromus* spp.); forbs; and C_4 grasses, and group ANPP was then estimated to explore any differential responses.

Experiment 2

To establish the differential effect of *P. glandulosa* on C_4 and C_3 grasses, shade/no-shade treatments only (Fig. 2: A, C, F, G, I) were repeated on heavily grazed 'short grass' areas where *B. dactyloides* dominated. Plant-level growth measurements and data analyses were similar to those described for *N. leucotricha*. However, because of the stoloniferous growth form and small basal area of *B. dactyloides*, the 'T-square' sampling technique (Krebs 1999), a measure of distance between neighbors which calculates plant density (plants·m^{-2}), was used for this species rather than measuring basal area growth.

Distance to nearest neighboring plant was defined as nearest separate stolon or rooted tuft. The disadvantage of this technique while not allowing direct comparison of absolute measurements would reveal any contrasting treatment responses by the two grass species.

RESULTS

Due to the large number of contrast tests generated by the statistical analyses employed, the results of *N. leucotricha* and *B. dactyloides* experiments are overviewed first. This is followed by a description of results pertinent to each hypothesis. Except where indicated statistical significance indicates alpha ≤0.05.

Overview

N. leucotricha plots - The significant difference of plot and individual plant production between natural and synthetic shade in 1998 indicated that the fabricated shade structure did not adequately simulate the effect of a natural canopy (Tables 3 & 4). The possibility that this was due to poor water permeability of the shade structures during 1998, which had unusually low rainfall, prompted a design modification for the 1999 season.

In 1998 *N. leucotricha* experienced negative changes of tillers/plant, (i.e. net tiller mortality) and basal area (Fig. 5). However, there were no other significant contrasts in ANPP, shoot production (Fig. 5) or any other measured variables for *N. leucotricha* plots (Tables A1, A2, A3 & A4)

In 1999 *N. leucotricha* ANPP did not exhibit any significant contrast response (Table A5; Fig. 6). Examination of species composition shows a significant contribution to herbaceous production by annual (mainly exotic) grasses. Comparison of estimated mean ANPP of annual grasses and *N. leucotricha* indicated a symmetrical response on interstitial sites, with highest production of N*. leucotricha* occurring in the absence of belowground competition (Fig. 7; treatment G & H).

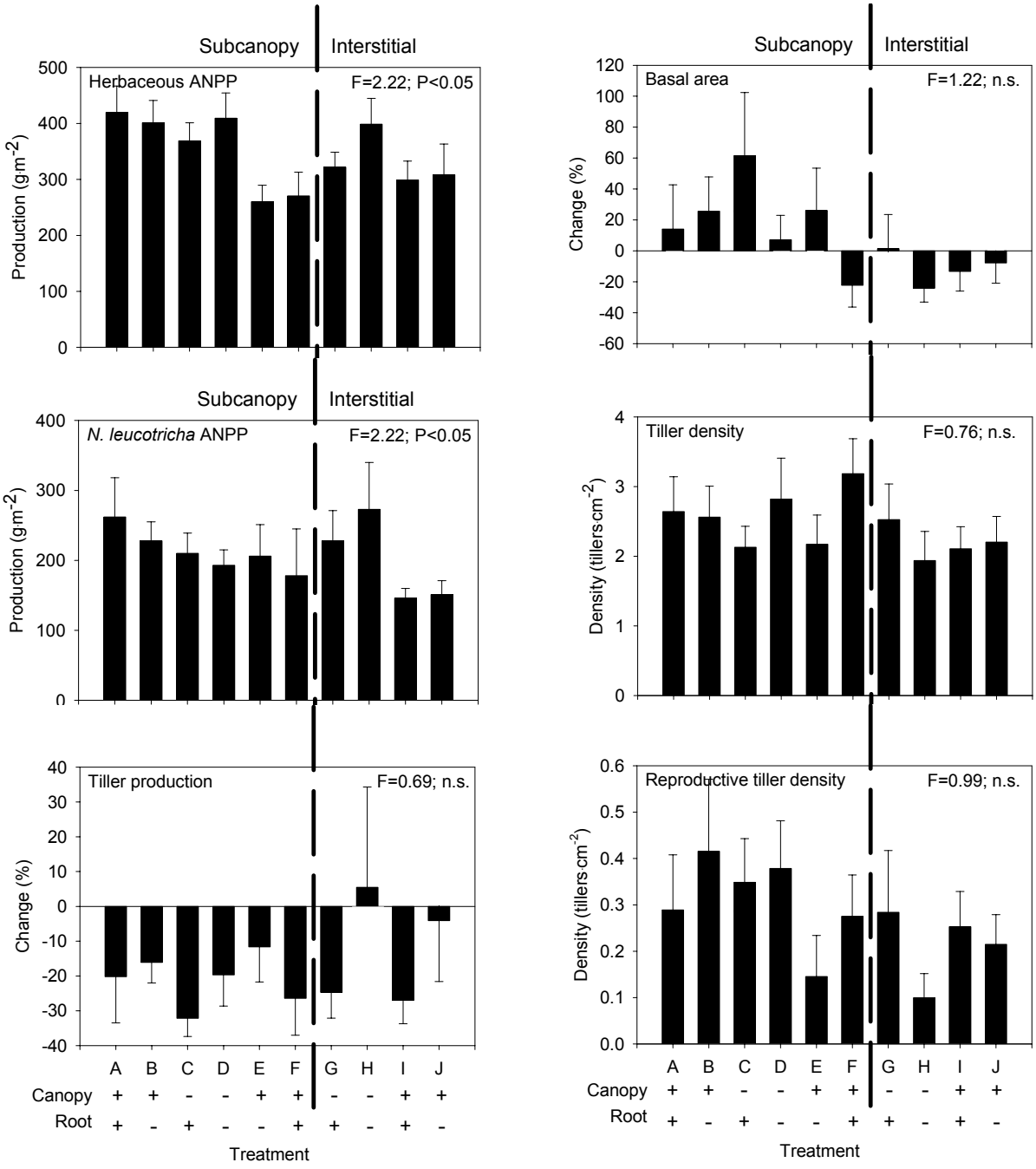

Fig. 5. Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and relative basal area growth per plant (from start to end of the growing season), tiller density, and reproductive tiller density, response to competitive treatments for midgrass sites in 1998 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition).

Table 3. Multiple contrasts for 1998 mid-grass plot ANPP, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526), ** (P < 0.05 with Bonferroni correction P < 0.00263), and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**P**
	model	9	2.22	0.0305**
1	subcanopy v gap	1	0.77	0.3841
2	+above v -above	1	3.37	0.0707
3	+below v -below	1	0.57	0.4520
4	+above +below v -above -below	1	3.99	0.0497
5	+above +below v -above +below	1	0.18	0.6744
6	+above -below v -above -below	1	4.73	0.0331
7	sub +below v -below	1	0.01	0.9116
8	sub +above v -above	1	2.12	0.1499
9	sub +above +below v -above -below	1	1.66	0.2025
10	gap -below v +below	1	1.12	0.2931
11	gap +above v -above	1	1.93	0.1693
12	gap +above +below v -above -below	1	3.00	0.0878
13	sub -below v gap -below	1	0.01	0.9294
14	sub +below v gap +below	1	1.32	0.2542
15	sub -above v gap -above	1	0.51	0.4792
16	sub +above v gap +above	1	0.94	0.3357
17	natural shade v synthetic shade	1	12.78	0.0006**
18	natural shade v no shade	1	1.03	0.3133
19	synthetic shade v no shade	1	9.83	0.0025**

Table 4. Multiple contrasts for 1998 *N. leucotricha* shoot biomass ($g \cdot m^{-2}$), tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.00526$) ** ($P < 0.05$ with Bonferroni correction $P < 0.00263$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.00053$).

	Contrast	**d.f.**	**F value**	**P**
	model	9	1.54	0.1519
1	subcanopy v gap	1	1.14	0.2893
2	+above v -above	1	0.08	0.7777
3	+below v -below	1	1.12	0.2945
4	+above +below v -above -below	1	0.74	0.3915
5	+above +below v -above +below	1	0.30	0.5840
6	+above -below v -above -below	1	0.02	0.8817
7	sub +below v -below	1	1.22	0.2726
8	sub +above v -above	1	0.69	0.4084
9	sub +above +below v -above -below	1	1.28	0.2621
10	gap -below v +below	1	0.10	0.7532
11	gap +above v -above	1	0.64	0.4281
12	gap +above +below v -above -below	1	0.12	0.7346
13	sub -below v gap -below	1	0.19	0.6661
14	sub +below v gap +below	1	1.16	0.2853
15	sub -above v gap -above	1	0.04	0.8502
16	sub +above v gap +above	1	2.35	0.1297
17	natural shade v synthetic shade	1	8.43	0.0049*
18	natural shade v no shade	1	4.61	0.0352
19	synthetic shade v no shade	1	0.86	0.3572

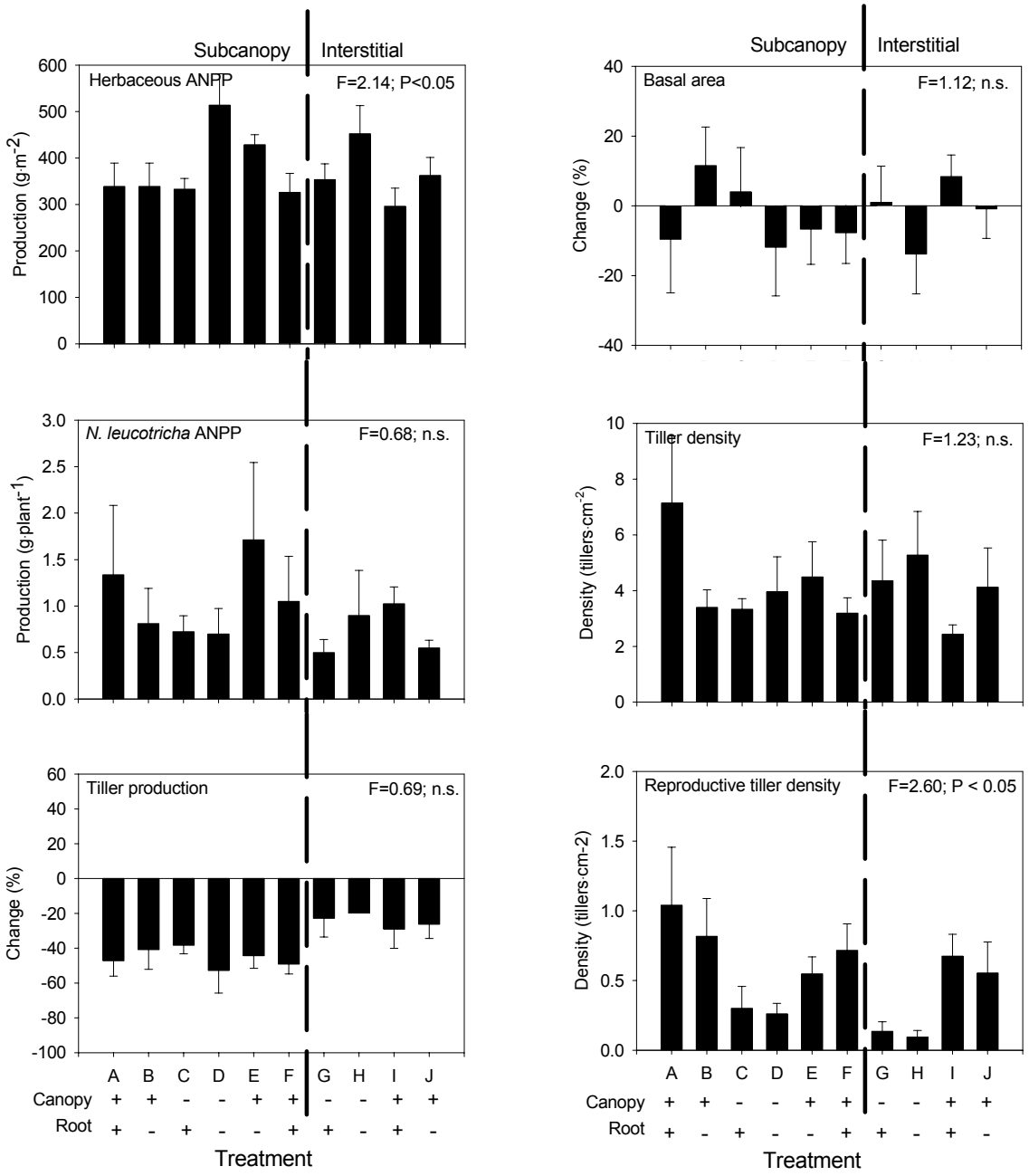

Fig. 6. Herbaceous ANPP, *N. leucotricha* ANPP, relative tiller production and relative basal area growth per plant (from start to end of the growing season), tiller density, and reproductive tiller density, response to competitive treatments for midgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition).

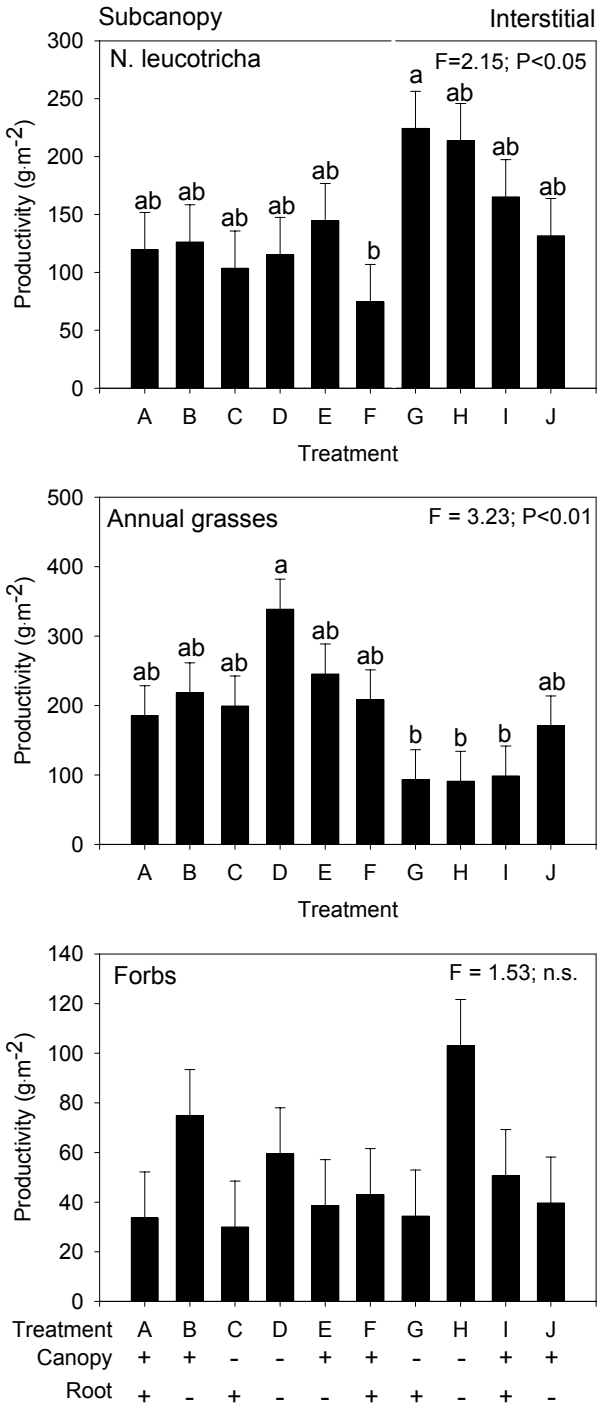

Fig. 7. ANPP estimated from dry-weight rank method of herbaceous groups response to competition treatments in 1999 (see Fig. 2 for treatment labels). Bars with different letters indicate significant difference at $P < 0.05$. Dotted line separates subcanopy from interstitial sites.

Comparison of functional group ANPP between subcanopy and open sites indicated annual grasses were relatively more productive below tree canopies where they produced more biomass than *N. leucotricha*, whereas *N. leucotricha* was relatively more productive in interstitial sites, where it produced more biomass that the annual grasses (Fig. 7, Table 5). Plot ANPP was greater in the absence of belowground competition and above- and belowground competition both in the subcanopy and interstitial sites (Table 6 contrasts 3, 4, 7, 9; Fig. 8 highlights the contrasts with significant differences). Relative change of tillers per plant and basal area and tiller density (Tables A6, A7, & A8) demonstrated no significant response to treatment. Only *N. leucotricha* reproductive tiller production showed any other competitive effect (Table 7; Fig. 9 highlights the contrasts with significant differences), with greater reproductive tillering under shade conditions with and without belowground competition.

B. dactyloides plots - Growth on C_4 dominated shortgrass sites was minimal during both seasons due to the summer drought conditions exhibiting tiller mortality in 1998 (Fig. 10). However, in the presence of shade there was a slight ($p < 0.10$) increase in *B. dactyloides* plot ANPP on sub-canopy sites in 1998 (Table 8; Fig 11). Although 1999 brought higher summer rainfall, growth parameters were highly variable (Fig. 12), and consequently, there were few significant differences in any contrasts during the study period (Tables A9 – A16) with the exception of lower ($P < 0.10$) *B. dactyloides* vegetative tiller density on subcanopy sites in 1999 (Table 9 contrast 1; Fig. 12 &13).

Hypotheses

Belowground competition (H1) - Total plot ANPP on *N. leucotricha* sites was significantly greater in the absence of belowground competition and above- and belowground competition both in the subcanopy and interstitial sites, but only in

Table 5. Summary of ANOVA results of ANPP (dry-rank weight method) for site (subcanopy vs. interstitial) and functional group (*N. leucotricha*, annual grasses, forbs) main effects and interactions in 1999.

	d.f.	**F value**	**P**
Site	1	2.42	n.s.
Functional group	2	40.08	<0.000001
Site*functional group	2	12.35	0.00001

Table 6. Multiple contrasts for 1999 mid-grass ANPP tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.00526$) ** ($P < 0.05$ with Bonferroni correction $P < 0.00263$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.00053$).

	Contrast	**d.f.**	**F value**	**P**
	model	9	2.14	0.0370**
1	subcanopy v gap	1	0.85	0.3588
2	+above v -above	1	3.02	0.0865
3	+below v -below	1	11.66	0.0011**
4	+above +below v -above -below	1	14.14	0.0003***
5	+above +below v -above +below	1	0.16	0.6893
6	+above -below v -above -below	1	4.23	0.0434
7	sub +below v -below	1	10.62	0.0017**
8	sub +above v -above	1	1.30	0.2575
9	sub +above +below v -above -below	1	10.53	0.0018**
10	gap -below v +below	1	1.98	0.1636
11	gap +above v -above	1	2.60	0.1111
12	gap +above +below v -above -below	1	4.56	0.0361
13	sub -below v gap -below	1	1.79	0.1847
14	sub +below v gap +below	1	0.00	0.9736
15	sub -above v gap -above	1	0.20	0.6552
16	sub +above v gap +above	1	1.54	0.2192
17	natural shade v synthetic shade	1	0.43	0.5143
18	natural shade v no shade	1	0.74	0.3933
19	synthetic shade v no shade	1	3.44	0.0678

Table 7. Multiple contrasts for 1999 *N. leucotricha* reproductive tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**P**
	Model	9	2.60	0.0120*
1	subcanopy v gap	1	4.47	0.0381
2	+above v –above	1	16.52	0.0001***
3	+below v –below	1	0.95	0.3323
4	+above +below v -above –below	1	11.91	0.0010**
5	+above +below v -above +below	1	11.37	0.0012**
6	+above -below v -above –below	1	5.64	0.0203
7	sub +below v –below	1	0.87	0.3530
8	sub +above v –above	1	8.14	0.0057
9	sub +above +below v -above –below	1	6.11	0.0159
10	gap -below v +below	1	0.16	0.6916
11	gap +above v –above	1	6.04	0.0165
12	gap +above +below v -above –below	1	4.08	0.0473
13	sub -below v gap –below	1	1.68	0.1997
14	sub +below v gap +below	1	2.87	0.0946
15	sub -above v gap –above	1	0.89	0.3474
16	sub +above v gap +above	1	1.23	0.2718
17	natural shade v synthetic shade	1	4.27	0.0424
18	natural shade v no shade	1	19.43	0.0001***
19	synthetic shade v no shade	1	8.22	0.0055

Table 8. Multiple contrasts for 1998 short-grass ANPP, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**P**
	Model	4	2.05	0.1087
1	subcanopy v gap	1	3.99	0.0535
2	+above v –above	1	0.61	0.4395
8	sub +above v –above	1	2.70	0.1090
11	gap +above v –above	1	1.45	0.2369
15	subcanopy -above v gap –above	1	0.07	0.7954
16	subcanopy +above v gap +above	1	7.47	0.0098*
17	natural shade v synthetic shade	1	1.37	0.2501
18	natural shade v no shade	1	1.86	0.1817
19	synthetic shade v no shade	1	0.06	0.8145

Table 9. Multiple contrasts for 1999 *B. dactyloides* tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**P**
	Model	4	2.06	0.1071
1	subcanopy v gap	1	7.87	0.0081*
2	+above v –above	1	0.91	0.3469
8	sub +above v –above	1	0.05	0.8247
11	gap +above v –above	1	0.25	0.6236
15	subcanopy -above v gap –above	1	3.72	0.0618
16	subcanopy +above v gap +above	1	3.53	0.0685
17	natural shade v synthetic shade	1	0.49	0.4899
18	natural shade v no shade	1	1.38	0.2476
19	synthetic shade v no shade	1	0.34	0.5619

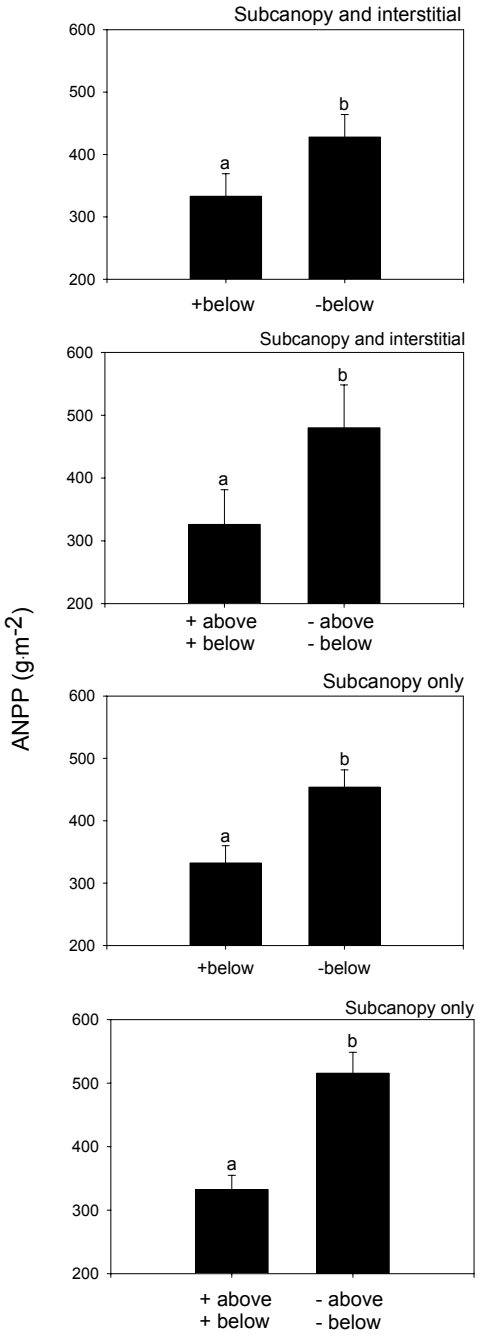

Fig. 8. Mean (± SE, n = 8) herbaceous ANPP in the presence and absence of above- and belowground competition for subcanopy and interstitial midgrass sites during 1999. Panel titles denote data pooling corresponding to statistical contrasts. Bars with different symbols are different at the $P < 0.05$ level.

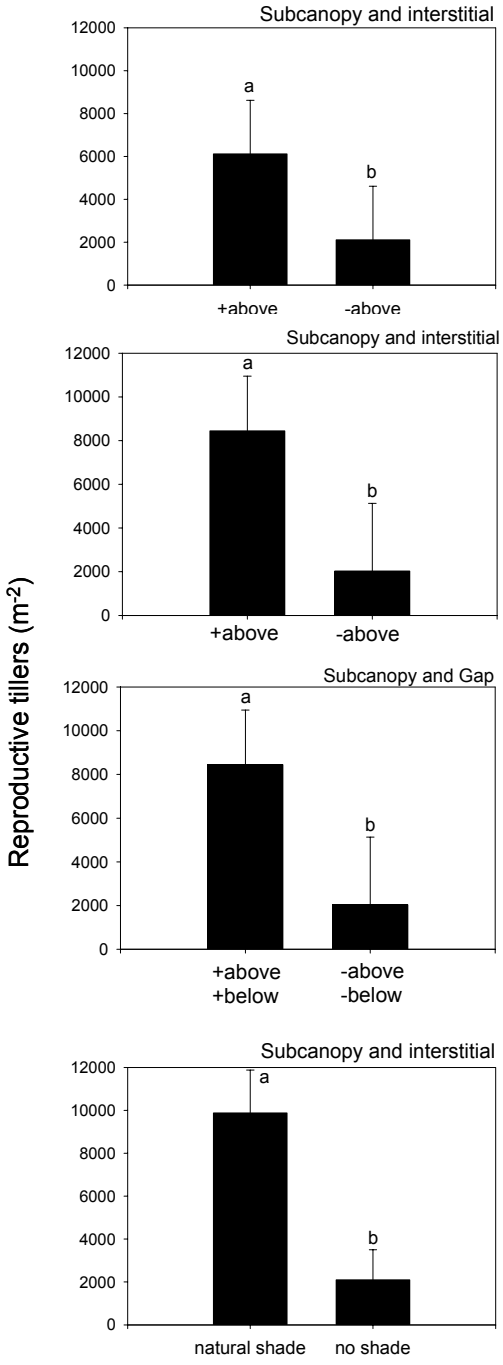

Fig. 9. Mean (± SE, n = 8) of *N. leucotricha* reproductive tiller density in the presence and absence of above- and belowground competition for subcanopy and interstitial midgrass sites during 1999. Panel titles denote data pooling corresponding to statistical contrasts. Bars with different symbols are different at the $P < 0.05$ level.

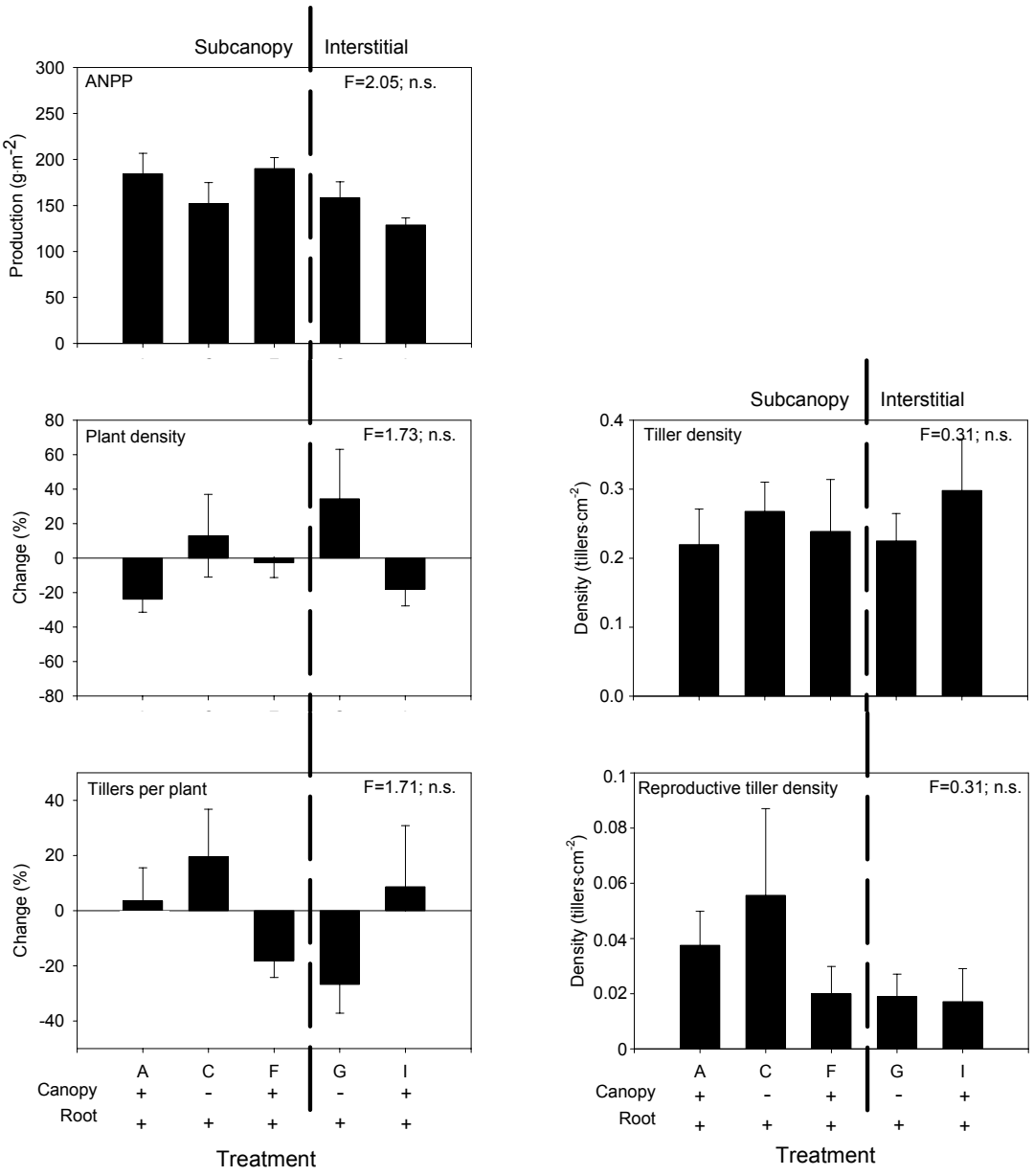

Fig. 10. Herbaceous ANPP, *B. dactyloides* plant density, relative tiller production, tiller density, and reproductive tiller density, response to competitive treatments for shortgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition).

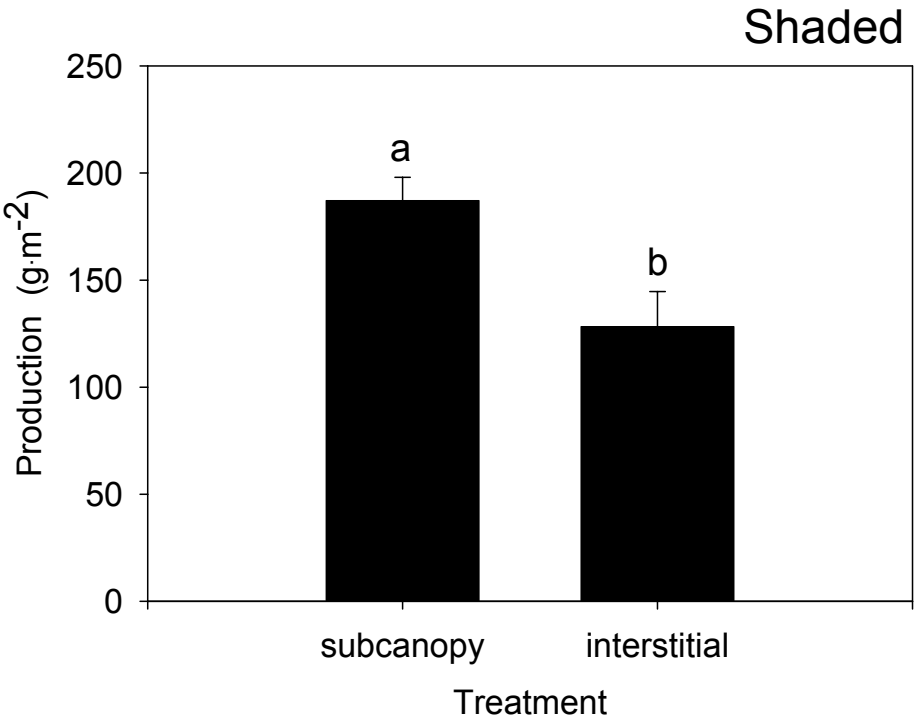

Fig. 11. Mean (± SE, n = 8) total shortgrass plot herbaceous ANPP in the presence of aboveground competition for subcanopy and interstitial shortgrass sites during 1998. Bars with different symbols are different at the $P < 0.10$ level.

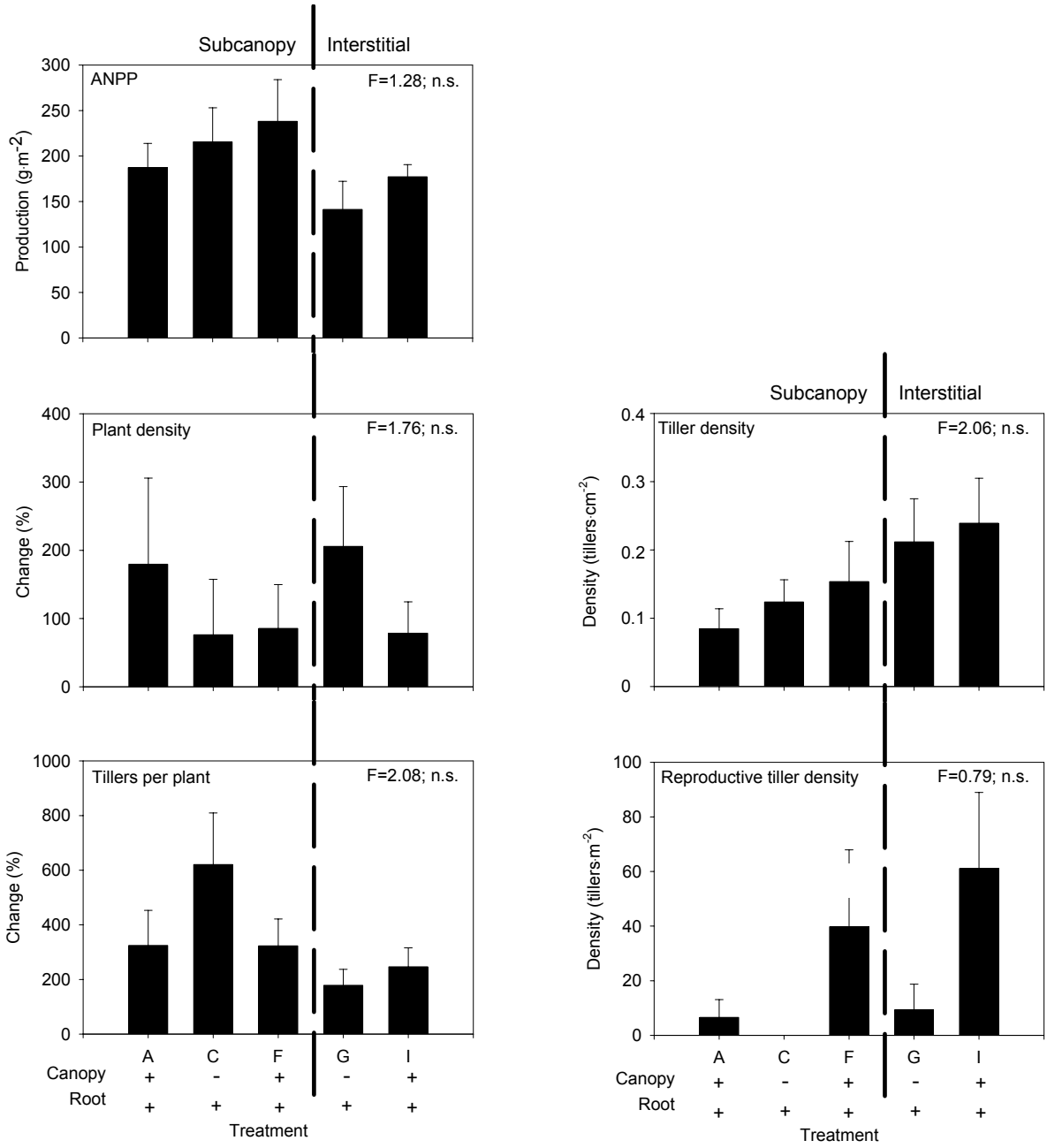

Fig. 12. Herbaceous ANPP, *B dactyloides* plant density, relative tiller production, tiller density, and reproductive tiller density, response to competitive treatments for shortgrass sites in 1999 (see Fig. 2 for treatment labels; +/- represents presence/absence of competition).

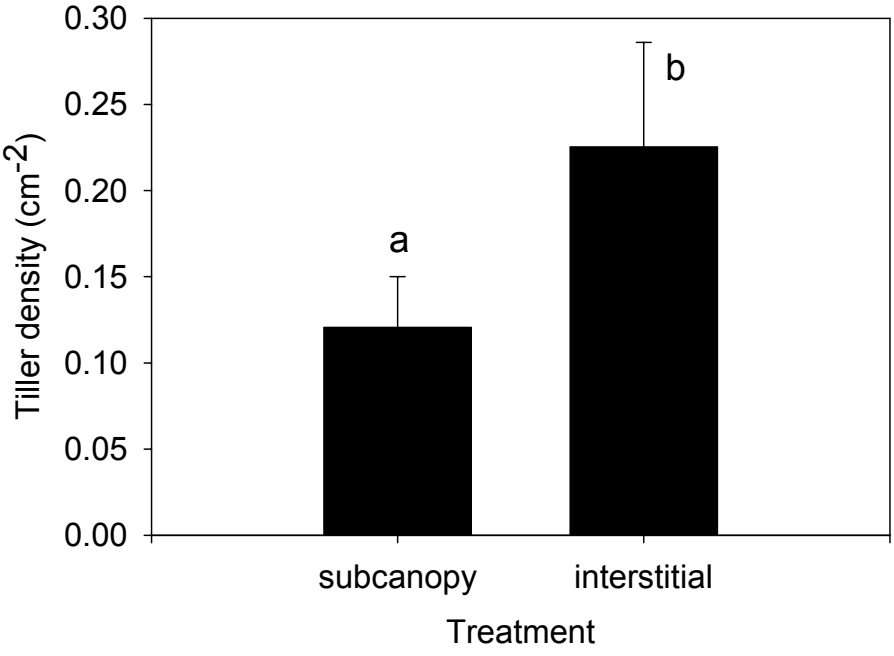

Fig. 13. Mean (±SE, n = 8) *B. dactyloides* tiller density for subcanopy and interstitial during 1999. Bars with different symbols are different at the P < 0.10 level.

1999 (Table 6 contrasts 3, 4, 7, & 9; Fig. 5, 6, & 7). However, other metrics did not reflect this response.

Fertile island effect (H2) - There was no significant difference of growth parameters between subcanopy and interstitial sites in either year on *N. leucotricha* sites. There was a slight ($P < 0.10$) depression of *B. dactyloides* tiller density on subcanopy sites in 1999 (Table 9 contrast 1; Fig. 13).

Canopy effect (H3) - Shade alone did not affect any of the vegetative growth parameters for productivity for either C_3 or C_4 grasses in either year. However, there was a greater density of *N. leucotricha* reproductive tillers under natural tree-canopy shade tillers in 1999 (Table 7 contrasts 2, 4, 5, 18; Fig. 9*)*

C_4 response (H4) - C_4 site response was largely neutral, with the exception of a small ($P < 0.10$) increase in *B. dactyloides* ANPP in 1998 on shaded subcanopy sites (Table 8 contrast 16; Fig 11).

DISCUSSION

There were few indications of any competitive or facilitative interactions between trees and grasses. Most responses were neutral suggesting that any combined positive and negative influences due to the presence of trees resulted in no net response. The only underlying mechanisms indicated by this study that might control herbaceous productivity were competition rather than facilitation, and the competition component was predominantly below-ground.

Belowground competition (H1)

Removal of belowground competition had the greatest overall effect in increasing plant production in the C_3 dominated sites (Table 6). Consequently it is deduced that belowground competition between trees and grasses had an

overriding role in explaining herbaceous production. McDaniel et al. (1982) demonstrated that when the *P. glandulosa* canopy cover rises above 15-20% herbaceous productivity declines. Similarly, in huisache savannas in south Texas *N. leucotricha* production declines above 25% tree cover (Scifres et al. 1982). Scifres and Polk (1974) attributed this result to an increase in overall competition without specifying whether this was above- or belowground. Others (Heitschmidt et al. 1986, McDaniel et al. 1982) have ascribed increase in overall herbaceous productivity following *P. glandulosa* removal to grass and forb response in the subcanopy region rather than interstitial areas. These data indicate that relaxing of the belowground competition between tree and herbaceous roots may have been the principal mechanism behind this response (Table 6, Fig. 8), supporting H1. Although competition was evident in subcanopy and interstitial locations combined, the greatest contribution was from the subcanopy sites (Fig. 8). This could be due to more intense tree-grass competition below-ground due to higher *P. glandulosa* fine root densities in the subcanopy, or that any fertile island effect may have amplified this effect. However, there was no other supporting evidence for the latter explanation. The lack of a similar response during the first year may be due to the reduction of spring rainfall. Belsky (1994) suggested that in a semi-arid East African savanna subcanopy competition would be greater at wetter sites particularly where the lateral spread of tree roots is confined to tree canopy.

Annual grass effect

The response of the C_3 annual grasses to manipulation of *P. glandulosa* above- and belowground competition was different to that of the C_3 perennial grass *N. leucotricha.* While *N. leucotricha* productivity increased slightly where *P. glandulosa* root competition was reduced in interstitial sites (Fig. 7), the annual C_3 grasses had higher mean productivity in competition alleviation treatments in the subcanopy patches, even though there is limited overlap of

growth period of these grass species and *P. glandulosa*. The exotic *B. japonicus,* the dominant annual grass at this site, has been shown to be a very strong competitor, and may have damped the response of other (C_3) species especially in the subcanopy, where it is frequently the dominant spring grass (Whisenant and Uresk 1990, Haferkamp et al. 1998). Spring rains strongly favor the fitness of exotic cool-season annual grasses, which are now a widespread component of mixed prairie communities (Whisenant and Uresk 1990, Haferkamp et al. 1998). The unusual climate of 1998/99, resulted in a greater contribution from cool season grasses and forbs than from warm season grasses, which demonstrated little seasonal growth overall and no treatment response whatsoever (Tables A9 – A16). This may be because these exotic annual species may have had a significant negative competitive effect on the indigenous grasses (Haferkamp et al. 1995, Haferkamp et al. 1998). Therefore the annual rather than the perennial grass component largely accounted for the competitive response in the subcanopy. Because the dominant C_3 annual grasses are exotic, invasive species, I speculate that in their absence, the native *N. leucotricha* would probably have exhibited a similar response at least in the subcanopy environment.

Fertile island effect (H2)

The lack of herbaceous response due to site (subcanopy versus interstitial), implies that if *P. glandulosa* modified the sub-canopy environment as previously suggested by other studies, then this characteristic did not affect the dominant perennial grasses during this study period. However, there is an indication that annual grass productivity was generally higher in subcanopy sites, while *N. leucotricha* productivity (1999) and *B. dactyloides* tiller density (1998) was marginally elevated in interstitial areas (Fig. 7 & 13). These combined but contrasting responses may have masked an overall herbaceous response to site treatment, but supports the concept that the presence of *P.*

glandulosa increases landscape heterogeneity, providing additional niches for different herbaceous functional groups.

Canopy effect (H3)

The lack of any vegetative response to the canopy suggests that any positive ameliorative effect of shade (e.g. on transpiration) may overshadow deleterious effects associated with canopy interception of rainfall or reduction in PAR. Although PAR reduction may have impacted C_4 grasses it is unlikely that shading by *P. glandulosa* canopy would have had significant negative effect of C_3 production because C_3 grasses grow when *P. glandulosa* is dormant.

Although the drought conditions during this study may have effected the responses, these results force the conditional refutation of the hypothesis of canopy effect on herbaceous growth, with the exception of the marked increase in allocation to reproductive tillers by *N. leucotricha* under shade during 1999. Reproductive tiller production is not uncommon in grasses particularly those exhibiting shade adaptation (e.g. Naumburg et al. 2001) and has been attributed to a response to low R:FR ratios under plant canopies (Ballaré and Casal 2000).

C_4 response (H4)

The lack of treatment response of the C_4 (*B. dactyloides* dominated) sites was probably due to the unusually dry summer during the study period. Shaded subcanopy shortgrass plot production was marginally ($p < 0.10$) higher than shaded interstitial but this may have been a result of inadequate shade construction during 1998 (Table 3) rather than any amelioration effect (Fig. 11). In a previous tree-removal study in the same area, Scifres and Polk (1974) indicated that grass layer response may occur only during normal rainfall seasons, and during dry years some treatment effects may be masked. The differential response of the C_3 versus C_4 sites may emphasize the dynamic fluctuation in dominance of species with different photosynthetic pathways

adjusts in response to annual climatic variation. It can be envisaged that C_4 sites may experience similar competitive response to the C_3 sites during a wetter summer growing season. Due to the overriding effect of climate in this study this hypothesis could not be adequately tested.

Implications for savanna models

This study provides only inferential evidence for any fertile island effect (H2) and apart from reproductive tiller production, no data to support any tree-shading effect on subcanopy environment (H3). To some extent the latter outcome may have been different if significant summer rainfall had occurred, thereby providing herbaceous growth during the warmer months where shading effects may have had a potentially stronger effect. Similarly, greater than normal annual grass production, especially in 1999, may have masked C4 response. But under conditions of below- average rainfall, any facilitative or competitive effects were either antagonistic or ineffectual. However, we can propose that belowground competition (H4) between *P. glandulosa* and grasses on these soils may be a key mechanism controlling the equilibrium of the two growth forms in this system, but may depend on temporal patterns of precipitation. The contribution from the C_3 grasses in this study suggests that belowground competitive interactions may play an important role given adequate rainfall. Callaway (1997) has suggested that competition occurs under benign abiotic conditions and is absent when resources are really low or high. The largely neutral responses from this study indicating an absence of evidence for facilitation, and presence and absence of competitive interactions in two climatically different years in this study supports this theory, but raises the question ‘under what conditions do competition or facilitation occur in this system?’ and requires a similar study to be conducted during both normal and wet years.

CHAPTER IV

HERBACEOUS UNDERSTOREY EFFECTS ON GROWTH OF THE TREE (*PROSOPIS GLANDULOSA*) LAYER IN A TEMPERATE SAVANNA

INTRODUCTION

Interactions between grasses and woody plants have been the subject of numerous studies in savannas. The vast majority of studies have examined the effect of trees on grasses; few have looked at the effect grasses might have on adult trees (Scholes and Archer 1997). The grass layer can interact directly with trees through resource competition, or indirectly through the intermediary effects of fire, which may induce tree mortality, particularly seedling (Menaut et al. 1990) or damaged (Yeaton 1988) trees, and post-burn alteration of soil resources benefiting surviving trees (Jensen et al. 2001). The response to presence of the herbaceous layer on woody plant seedlings and adult trees ranges from neutral (Brown and Archer 1989, McPherson and Wright 1989) to negative (Stuart-Hill and Tainton 1989, De Steven 1991, Archer 1995a, McPherson 1997). Existing research suggests that shallower rooted grasses may actively compete with trees for resources during a wet season (Ehleringer et al. 1991, Dawson and Pate 1996) either directly, if they coincide with tree roots in the soil profile, or indirectly, intercepting water and nutrients and reducing their percolation to deeper portions of the soil profile where tree roots are concentrated. If this model is correct, then disturbances that reduce above and/or belowground production in the herbaceous layer (e.g. fire, grazing) and hence plant utilization of soil resources should benefit tree growth.

Soil characteristics may indirectly influence root interactions of trees and grasses. Studies from southern Africa suggest that existence of grass-tree competition may be a function of soil type, whereby the intensity of herbaceous competition is relaxed on coarse-textured soils where water can percolate

deeper through the soil profile and more intense on fine-textured soils where water is more likely to be retained in upper soil horizons (Knoop and Walker 1985). However, grazing, by reducing above- and belowground biomass, may neutralize the competitive suppression of tree growth by grasses (Stuart-Hill and Tainton 1989). Alternatively, where the available soil volume is low, as on shallow soils, woody and herbaceous roots are concentrated in the same volume with little opportunity for vertical segregation. Research in North Texas savannas has demonstrated that *P. glandulosa* trees may rely heavily on lateral roots, which permeate interstitial spaces, particularly where available soil volume is reduced (Ansley et al. 1990, Ansley et al. 1991, Ansley et al. 1992a, Cuomo et al. 1992, Heitschmidt et al. 1988). In these situations, grasses, with their relatively dense, shallow root systems should be better situated to acquire soil resources and effects of grasses on tree growth should be maximized. Herbaceous effects on tree growth may therefore be inversely proportional to soil depth.

Many savannas around the world are sustained by fire (Jensen et al. 2001). Fire frequency in many systems may be disrupting the savanna equilibrium by not only effecting species composition but also soil nutrient status (Dumontet et al. 1996, Jensen et al. 2001). The role of fire in maintenance of savannas ranges from one of completely excluding woody plants, to one of modifying structure of savannas dominated by fire-tolerant woody species (Scholes and Walker 1993). Consequently, most savanna research regarding the effect of fire on woody plants has examined seedling mortality and vegetative regeneration of established adult trees. However, individuals of larger stature often escape with minimal canopy damage (Menaut et al. 1990, Scholes and Walker 1993). Fire is to known to enhance post-fire tree seedling establishment by increasing available nitrogen (N), phosphorus (P), potassium, calcium, and magnesium in the mineral soil (Christensen 1977, McKee 1982, Covington and Sackett 1984, Schoch and Binkley 1986, Jensen et al. 2001).

Consequently, it has been proposed that low intensity understorey fires will stimulate growth in fire resistant adult trees (de Ronde et al. 1990). However, this hypothesis has yet to be tested.

Hypotheses

Shallow grass roots actively compete with trees for resources either directly, if they coincide with tree roots in the soil profile, or indirectly, intercepting water and nutrients, and reducing their percolation to deeper portions of the soil profile where tree roots are concentrated. If this is true, then:

H1(a) - Tree growth will be enhanced due to understorey herbaceous reduction following mowing or
H1(b) - complete removal resulting from herbicidal treatment.

Coincidence of tree and herbaceous roots is more likely where soil volume is reduced. Therefore:

H2 - Tree growth response to herbaceous manipulation will be greater on shallower soils.

Post-fire modification of the upper portion of the soil profile may temporarily reduce herbaceous competition and increase soil resources of potential benefit to surviving trees.

H3 - Tree growth will be enhanced following low intensity burning of the herbaceous layer.

METHODS

To experimentally test whether the presence of the herbaceous layer affects tree growth, three treatments (control, herbaceous defoliation and sward removal) were applied within a 5-m radius of randomly selected *P. glandulosa* trees (five replicates per treatment) at the Nine-mile (deep: 3–4 m), Four-corners (intermediate: 2–3 m) and Hazelwood (shallow: 1–1.2 m) pastures. An early spring (March 1998 and 1999) repeated burn treatment was also applied at the deep and intermediate soil depth sites, but not at the shallow soil site for logistic reasons. Fuel loads for the burn treatments were approximately 1200 $kg \cdot ha^{-1}$ during 1998 but between 500-700 $kg \cdot ha^{-1}$ the following year. Flame lengths ranged from 30-100 cm at both deep and intermediate soil depth sites. Defoliation was achieved using a hand operated, gasoline-powered mower at a frequency necessary to maintain a 3-6 cm stubble height. Sward removal was achieved by killing herbaceous vegetation with the general glyphosate herbicide (Roundup ®), with follow-up spot treatments applied as necessary. Response variables included soil moisture, *P. glandulosa* basal area growth, and foliar P and N concentrations.

P. glandulosa basal growth was measured using dendrometer bands (Palmer and Ogden 1983) on larger trees, and calipers for smaller (<5 cm basal diameter) trees at locations marked with indelible ink. Initial basal area (cm^2) measurements were made in December 1997 with subsequent growth increments recorded using dendrometer bands in December 1998 and 1999. Nutrient acquisition was assessed by quantifying canopy foliage total P and N concentrations in July 1999. Four subsamples (each consisting of 8–10 leaves) were collected from the exterior of each tree canopy. These were transported to the laboratory, dried at 70ºC, ground to pass through a 1-mm mesh, acid digested, and colorimetrically analyzed for N (TNT persulphate digestion method, Hach Compnay 1998) and P (acid persulphate method, Hach Company

1998) using a Hach DR/3000 spectrophotometer (Hach Company, Loveland, Colorado).

Soil moisture was measured to 1.5 meters using neutron scattering (Model 3220 series soil moisture gauge, Troxler Electronic Laboratories, Research Triangle Park, North Carolina) (Pearcy et al. 1996) on deep and shallow soil sites. To avoid any interaction with tree canopy, aluminium access tubes (diameter 5.08 cm) located 4 m from the tree stem axis were inserted in pre-drilled holes to a depth of 1.5 m. Volumetric soil moisture readings were taken at five depths (where soil depth allowed) at 30-cm intervals (probe center at 25, 55, 85, 115, 145 cm). To assess any horizontal surface moisture gradient from tree axis, near-surface (0-30 cm) volumetric soil moisture was assessed with Time Domain Reflectometry (TDR) (Topp et al. 1984, Topp and Davis 1985). Paired 4-mm steel probes, were positioned 5 cm apart, at three intervals (1, 2, and 4 m) horizontally from tree axis.

ANOVA and repeated measures ANOVA using SAS (SAS Institute Inc. 1988) and NCSS (Number Cruncher Statistical System, Hintze 2001), was used to compare tree growth rates, leaf-nutrient concentrations, and changes in soil moisture with depth and time. Except where indicated statistical significance indicates alpha ≤ 0.05. Tukey's multiple comparison test (alpha ≤ 0.05) was used throughout to compare means (Zar 1999).

RESULTS

P. glandulosa stem basal area and absolute basal growth rates were lowest on the shallow soil site and highest but comparable on the sites with intermediate and deep soils (Table 10). Absolute annual basal growth ($cm^{2} \cdot y^{-1}$) was directly related to initial stem size for all sites and both years (Table 11), therefore relative growth rates ($cm^{2} \cdot cm^{-2} \cdot y^{-1}$) were used for statistical analysis.

Rainfall in 1998 (504 and 427 mm on deep and shallow sites, respectively) was lower than that received in 1999 (560 and 614 mm) and both

Table 10. Means and standard errors of initial stem basal area and absolute annual basal area growth rate of *P. glandulosa* trees at shallow, intermediate, and deep soil sites. Means with different letters indicate differences at $P < 0.01$.

	Initial basal area (pre-treatment)		Absolute basal area growth rate (controls only)		
	1997		1998	1999	
	n	Mean (±SE) cm^2	n	Mean (±SE) ($cm^2 \cdot yr^{-1}$)	Mean (±SE) ($cm^2 \cdot yr^{-1}$)
Shallow	15	55.5 (±4.2)[a]	5	1.47 (±0.35)[a]	2.38 (±0.44)[a]
Intermediate	20	206.9 (±20.0)[b]	5	5.69 (±1.01)[b]	7.02 (±1.38)[b]
Deep	20	182.7(±18.7)[b]	5	7.77 (±2.39)[b]	6.63 (±1.21)[b]

Table 11. Summary of regression results for the relationship between absolute annual growth rate ($cm^{2} \cdot yr^{-1}$) and initial basal area (cm^2) of *P. glandulosa* for soil depth (shallow, intermediate and deep) and year (1998, 1999).

Site	Year	R^2	P
Shallow soil	1998	0.49	< 0.0001
	1999	0.15	< 0.05
Intermediate soil	1998	0.56	< 0.0001
	1999	0.50	< 0.0001
Deep soil	1998	0.71	< 0.0001
	1999	0.76	< 0.0001

years were below the long-term average (665 mm) on both sites (Fig. 1 page 10). Monthly rainfall patterns were slightly different between sites. In 1998 the shallow soil site received no measurable rainfall from July through September, whereas the deep soil site received 49 mm during this period; conversely, the shallow soil site received more rainfall than the deep soil site in spring and late summer 1999 (Fig. 1, page 10).

Treatment effects on *P. glandulosa* growth varied among sites and between years (Table 12, Fig 14). Surface fire enhanced *P. glandulosa* growth relative to unburned controls, but only on the deep soil and only during the growing season immediately following the burn (1998, Fig. 14A).

Relative growth of *P. glandulosa* plants in the removal treatment was significantly greater at the shallow and intermediate soil depth sites compared to deep soil sites in 1999 (Table 12, Fig. 14B and C). In contrast, mowing demonstrated no equivalent effect on any site and in either year. Relative growth of plants on control plots was comparable between sites and years (ca. 0.1 $cm^{-2} \cdot cm^{-2} \cdot y^{-1}$) but plants on shallow soils tended to be most responsive to herbaceous manipulations and variations in annual rainfall.

There was no overall effect of site or depth in profile on soil water content, but time of year (date), herbaceous treatment effects, and interactions among site, depth, date, and treatment were significant (Table 13; Fig 15). Shallow sites exhibited more pronounced and different seasonal patterns of soil moisture stratification with depth in profile than did deep soil sites. On the deep soil site removal of the grass layer had no effect on the soil moisture profile. In contrast, soil moisture on herbaceous removal plots exceeded that on control plots during most dates in 1999. Surface soil moisture, as measured with TDR probes, showed a third-order interaction among site, treatment, and distance from tree bole (Table 14). Mean surface moisture was significantly higher where the herbaceous layer had been removed, but shallow soil sites had consistently lower water content for both treatments compared to deep soil sites (Fig 16).

Table 12. Summary of independent repeated measures ANOVA results for each soil depth for year (1998, 1999), and herbaceous manipulation treatment (control, mow, sward removal, burn) main effects and interactions on basal area growth of *P. glandulosa*.

	d.f.	F value	P
Deep soil			
Treatment	3	4.54	0.01
Year	1	8.04	0.01
Treatment*year	4	3.71	0.05
Intermediate soil			
Treatment	3	3.93	0.05
Year	1	6.30	0.05
Treatment*year	4	1.12	n.s.
Shallow soil			
Treatment	2	6.99	0.001
Year	1	0.70	n.s.
Treatment*year	4	1.75	n.s.

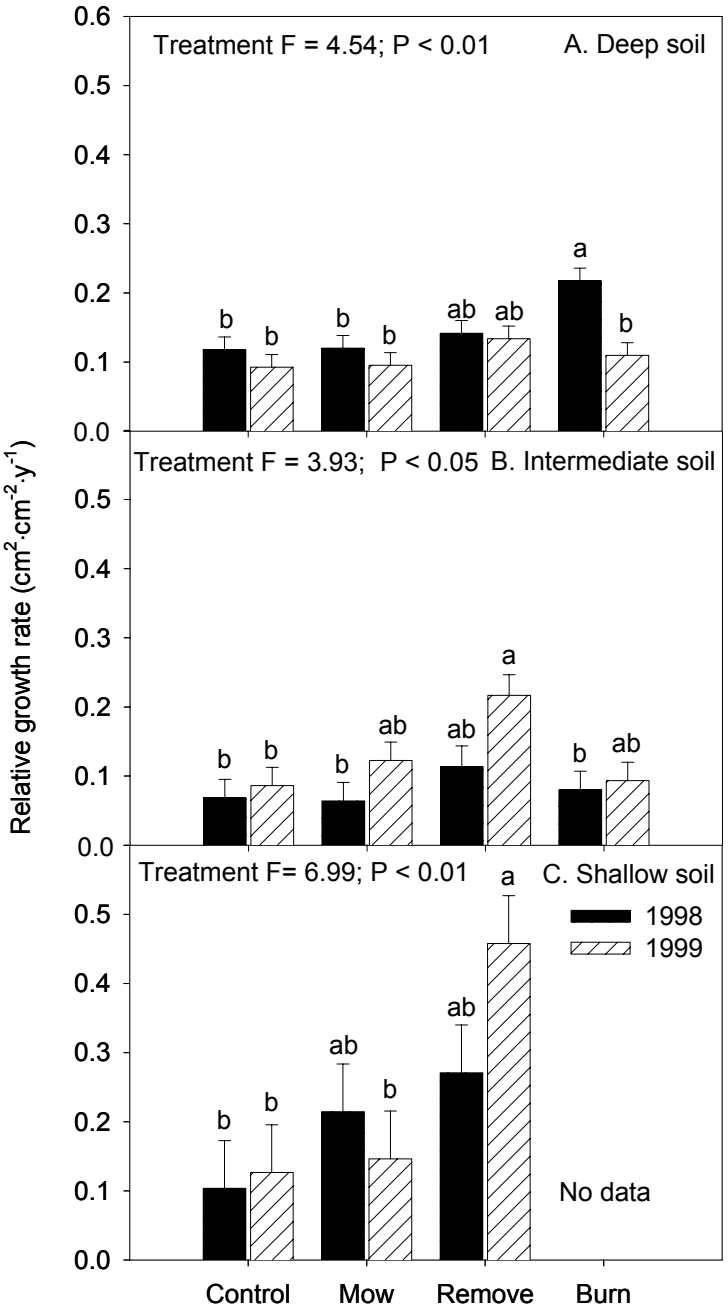

Fig. 14. Mean (± SE; n = 5) relative basal area growth of *P. glandulosa* trunks in response to understory manipulation (control = no treatment, mowed, remove = sprayed with herbicide, and burned) during 1998 (solid bar) and 1999 (hatched bar) on sites with contrasting soil depths. Results of repeated measures ANOVA shown for each site. For a given site, bars with different letters were significantly different at $P \leq 0.05$.

Table 13. Summary of repeated measures ANOVA results for site (shallow vs. deep soil), depth in soil profile (depth, 0-115 cm), date (month of year in 1999), and treatment (control, sward removal) main effects and interactions on soil moisture profiles during 1999.

	d.f.	**F value**	**P**
Site	1	0.44	n.s.
Treatment	1	24.70	0.0001
Site * treatment	1	10.83	0.01
Depth in profile	3	0.27	n.s.
Site * depth	3	5.13	0.01
Treatment * depth	3	1.10	n.s.
Site * treatment * depth	3	1.25	n.s.
Date	6	41.75	0.0001
Site * date	6	7.66	0.0001
Treat * date	6	0.72	n.s.
Site * treat * date	6	1.68	n.s.
Distance * date	18	1.40	n.s.
Site * depth * date	18	0.66	n.s.
Treat * depth * date	18	0.15	n.s.
Site * treat * depth * date	18	0.18	n.s.

Table 14. Summary of repeated measures ANOVA results for site (shallow vs. deep), treatment (control, mow, sward removal), distance from tree bole (1, 2, 4 m), and date (month of year, 1999) main effects and interactions on TDR measured surface soil moisture during 1999.

	d.f.	F value	P
Site	1	90.81	0.00001
Treatment	1	5.76	0.05
Site * treatment	1	0.01	n.s.
Distance from bole	2	4.48	0.05
Site * distance	2	1.19	n.s.
Treatment * distance	2	1.74	n.s.
Site * treatment * distance	2	6.90	0.01
Month	3	13.04	0.00001
Site * month	3	5.81	0.001
Treat * month	3	0.32	n.s.
Site * treat * month	3	0.16	n.s.
Distance * month	6	0.39	n.s.
Depth * distance * month	6	0.36	n.s.
Treat * distance * month	6	0.28	n.s.
Depth * treat * distance * month	6	0.13	n.s.

Table 15. Summary of ANOVA results for site (shallow, intermediate and deep soil), treatment (control, mow, sward removal) main effects and interactions on leaf N and P measured in 1999.

	d.f.	F value	P
Leaf N			
Site	2	4.07	0.05
Treatment	2	3.81	0.05
Site * treatment	4	0.32	n.s.
Leaf P			
Site	2	13.59	0.0001
Treatment	2	5.26	0.05
Site * treatment	4	3.36	0.05

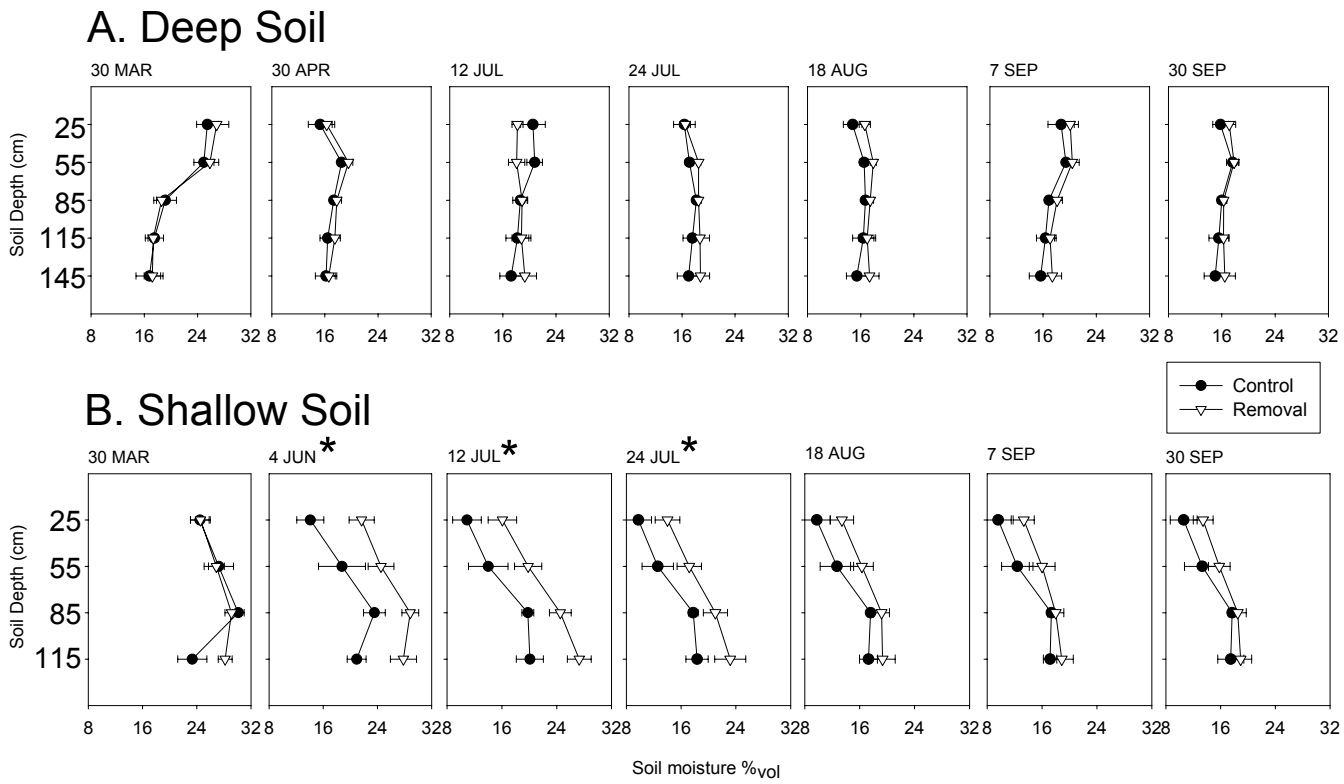

Fig. 15. Patterns of mean (± SE; n = 5) soil moisture (neutron scattering; volumetric) with depth on control plots (herbaceous layer intact; closed circles) and herbaceous removal plots (open triangles) on deep (A) and shallow (B) soils during the 1999 growing season. Asterisks indicate significant differences ($P \leq 0.05$) between control and removal moisture profiles. Readings were made 4 meters horizontally from *P. glandulosa* stem.

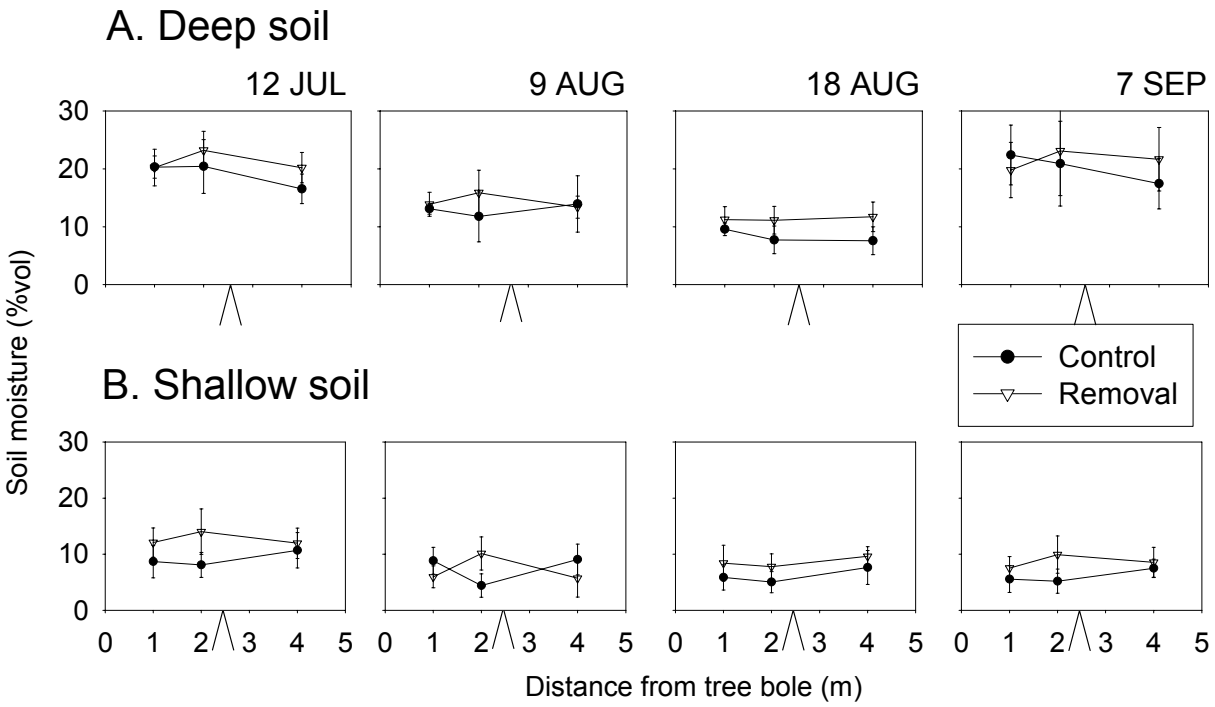

Fig. 16. Mean (± SE; n = 5) surface (30 cm) soil moisture (TDR; volumetric) at 1m, 2m, and 4m meters from *P. glandulosa* stems in 1999 on deep (A) and shallow (B) soil plots where the herbaceous layer was intact (control; solid circles) or removed (open triangles). Arrow represents average location of tree canopy drip-line.

The seasonal trends observed in the upper 30 cm of the soil profile was similar to that recorded by the neutron probe. The increase in soil moisture in September at the deep soil site reflects a rain event that occurred only at this site.

Mowing and removal of the herbaceous layer elicited an increase in *P. glandulosa* leaf N at the shallow soil site, but did not affect leaf N on intermediate and deep soil sites (Fig. 17A). Differences in leaf P among sites were more marked and the site-treatment interaction was significant (Table 15). At the deep soil site leaf P on the burn sites was greater than on control and mow treatments (Fig. 17B). However, at the intermediate soil depth site, levels of *P. glandulosa* leaf P subjected to mowing were elevated in comparison to those of plants on control plots. At the shallow soil site, trees subjected to herbaceous removal exhibited elevated ($P < 0.01$) leaf P levels relative to controls or trees with mown understories (Fig. 17B).

DISCUSSION

Although elsewhere *P. glandulosa* has been described as a phreatophyte able to extract deep soil moisture via taproots (see Ansley et al. 1992a for review), research in the Rolling Plains of Texas has indicated that this species also relies on shallow lateral roots for water extraction (Heitschmidt et al. 1988; Ansley et al. 1990; Ansley et al. 1991; Ansley et al. 1992a). In this region, small, intermittent summer rainfall events have little deep penetration and may be quickly lost to evapotranspiration (Ansley et al. 1990). These characteristics imply the potential coincidence of belowground resource acquisition with trees and herbaceous plants in this savanna system, and enhance the sensitivity of the tree component to competitive status of the herbaceous layer.

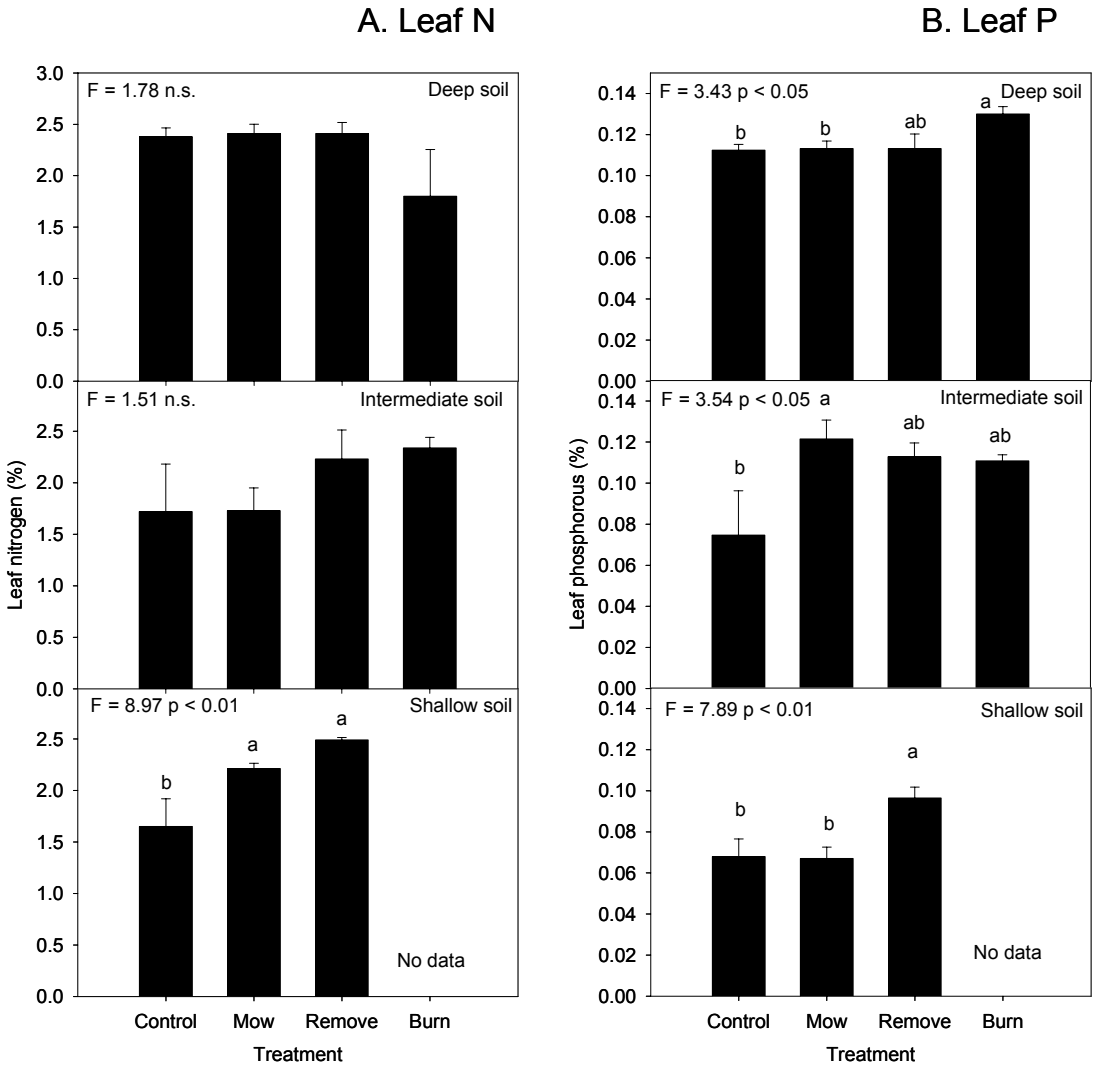

Fig. 17. Mean (± SE; n = 5) leaf N (A) and P (B) (% dry weight) of *P. glandulosa* plants in July 1999 in response to understory manipulation (control = intact; mown, remove = herbicided, burned) with contrasting soil depths. Bars with different letters denote significant differences at $P \leq 0.05$. Absence of letters denotes no significant difference between bars.

Sward removal

Increased tree growth in response to sward removal by herbicide observed on intermediate and shallow soil sites in 1999 (Fig. 14), may be due to the higher rainfall during this second growing year of study (Fig. 1) (Miller et al. 2001). In 1999 precipitation was greater at the shallow soil (614 mm) site than at the deep soil site (560 mm) and this could have had a confounding effect. However, the summer drought conditions experienced in 1999 resulted in a greater contribution to herbaceous production from the cool rather than warm season grasses (Chapter III), and during the spring growing period (February – June) precipitation was comparable at both sites (Shallow soil = 356 mm; Deep soil = 345). In a study on a savanna site in southern Africa, Knoop and Walker (1985) found that during drier years the competitive effect of the herbaceous layer was negligible. Given the magnitude of the response on the grass removal treatment on the shallow soils site during the second season, it is proposed that the competitive potential of the herbaceous layer is inversely related to soil depth but during dry years the productivity and hence competitive ability of this layer is suppressed. Although sward removal did not significantly alter soil moisture content on deep soils, it did appear to result in a conservation of moisture in the overall profile at the shallow soil depth site (Fig.15). The decreased probability of coincidence of tree and grass roots resulting in lower overall root density on deeper soils may have lowered transpirational consumption. Soil moisture was lower following sward removal at the end of spring, but this profile converged with control conditions as the summer progressed. Greater available soil moisture could have improved water status of individual trees and mobilization of soil nutrients resulting in greater relative growth rates following sward removal. However, the fact that soil moisture remained elevated suggests that tree roots could not take full advantage of increased water availability.

The lack of a significant tree response to mowing of the herbaceous layer has been observed elsewhere (Stuart-Hill and Tainton 1989). Given that sward removal did result in increased tree growth at the shallow and intermediate soil depth sites in 1999, it can be envisaged that more frequent and/or closer mowing and therefore grazing, might reduce the competitive ability of the herbaceous layer, resulting in a positive effect on tree growth.

Increased tree growth following herbaceous sward removal has been attributed elsewhere to interception of water (Knoop and Walker 1985), or reduction of competition for belowground space and nutrients (Stuart-Hill and Tainton 1989, Archer 1995a, McPherson 1997) or both. In this study, trees in the sward removal treatment demonstrated elevated leaf P and N at the shallow soil site (Fig. 17) suggesting woody and herbaceous plants may compete for nutrients as well as water. Although *P. glandulosa* has the ability to symbiotically fix N the elevated N status in trees in mow and sward removal treatments suggests that this process may be operating below capacity on the shallow soil site, possibly due to water limitation. Studies in south Texas (Archer 1995b, Barnes and Archer 1999) have already demonstrated that on shallower soils *P. glandulosa* becomes more vulnerable to belowground competition with other woody species. Where soil volumes are smaller the resources may be limiting and competitive interactions intensify due to increased dependence by *P. glandulosa* on shallow lateral roots. Equally, the lack of effect of grass removal on deep soils may be due to minimal tree-grass competition where a larger soil volume allows resource partitioning between the two growth forms. This hypothesis is supported by the greater effect of the removal treatments on increasingly shallower soils.

Fire

Burning at the deep soil site stimulated *P. glandulosa* growth following the first post-fire growing season, but not the second (Fig. 14A), despite the fact that

1998 was slightly wetter than 1999 (504 vs. 560 mm). This may reflect a response to a short-term post-fire nutrient flush in 1998; and a return to status-quo nutrient levels by the 1999 growing season. The process of burning has been shown to elevate overall soil nutrient availability via ash deposition and increased mineralization (Valmis and Gowans 1961, Christensen and Muller 1975, Reich 1983, Hobbs and Schimel 1984, de Ronde et al. 1990, Kauffman et al. 1994). These processes can enhance growth rates of vegetatively regenerating woody shoots, and stimulate flowering (Hodgkinson 1998), and root growth (Haase and Sackett 1996). Although leaf P was elevated at the deep soil sites there was no measurable difference of leaf N. P present in plant tissue is usually directly deposited in ash, however, plant N volatilization can occur at 200ºC and increase to 60% above 700ºC (MacLean et al. 1983), so N may have been lost even under low intensity burn conditions. Alternatively, any post-fire elevation of soil N may have been masked by adequate N supply due to the N_2-fixation ability of *P. glandulosa* (Zitzer et al. 1996). The lack of a tree growth or leaf nutrient response at the intermediate depth soil during 1998 is difficult to explain, unless water availability, which is necessary for nutrient mobilization, was a limiting factor on this shallower soil.

Implications for savanna models

Existing savanna models that attempt to explain the coexistence of the grasses and trees, acknowledge the importance of the interactions of fire, herbivory, water and soil characteristics. However, intensity of interspecific competition demonstrated by numerous studies (Scholes and Archer 1997) may favor a disequilibrium model, where the magnitude of biotic and abiotic forces shifts the biological advantage between these physiognomic types. It is however uncertain which of these mechanisms ultimately would have the greatest influence on savanna dynamics.

We can conditionally accept the proposed hypothesis that herbaceous removal will enhance tree growth on shallower soils where competition for both water and nutrients between these two growth forms will be more intense. Furthermore, increasing environmental stress due to drought or increased herbivory may initiate reduction in resource acquisition by the herbaceous layer (Chapin 1991), releasing competitive resource pressure and favor tree growth.

Existing studies suggest that periodic low intensity fire supports the savanna landscape by preferentially selecting against smaller plants thus controlling woody recruitment and by maintaining an herbaceous layer (Hochberg et al. 1994, Bond and van Wilgen 1996). However, it has been demonstrated that resprouting species like *P. glandulosa* may exhibit low post fire mortality even as seedlings (Ansley et al. 1994). The additional evidence from this study supports the hypothesis that low intensity fire may also reinforce the savanna tree-grass structure by enhancing the growth of existing adult tree through periodic reduction of competition with the herbaceous layer and generation of a short-term nutrient pulse.

CHAPTER V

BELOWGROUND INTRASPECIFIC COMPETITION OF HONEY MESQUITE (*PROSOPIS GLANDULOSA*) IN A TEMPERATE SAVANNA

INTRODUCTION

Knowledge of the mechanisms of controlling woody plant density is one key to potentially explaining the various patterns of tree distribution which occur in savannas (random, clumped, regular) and their various effects (positive, neutral or negative) on the composition and productivity of the herbaceous matrix. Intraspecific competition has been widely investigated in timber and agroforestry systems (e.g., Kenkel 1988, Shainsky and Radosevich 1992, Patch and Felker 1997, Villagra and Felker 1997, Baldwin et al. 2000), but little is known of the importance of this phenomenon for natural woodlands (Duncan 1991), and savannas (Scholes and Archer 1997). The vast majority of species interactions research in savannas has emphasized interspecific (inter-lifeform) interactions between woody and herbaceous components (House et al. 2003). Savanna physiognomy spans a continuum ranging from open grasslands with few trees through to woodlands. It can be envisaged that the effects of intraspecific competition of trees may become progressively more important in systems with higher tree densities.

The dynamic maintenance of savanna structure is controlled primarily by external abiotic (e.g. fire, soils, and rainfall), or biological (e.g. herbivory) (Skarpe 1992, Scholes and Walker 1993) factors and their interaction (Walker et al. 1981, Hochberg et al. 1994). The spatial distribution of savanna trees can therefore be difficult to explain (Manning and Barbour 1988, Jeltsch et al. 1996), and the influence of soils, topography and rainfall may influence or mask competitive interactions (San Jose et al. 1991, Archer 1995a, Jeltsch et al. 1996, Scholes and Archer 1997). The composition of the woody component of savannas is highly variable. There may be one dominant, or two or more

codominant trees or shrubs that characterize a particular savanna system (e.g. McPherson 1997, Scholes and Archer 1997), but which coexist with other canopy or subcanopy woody species. Therefore, with some exceptions (e.g. the longleaf pine and mesquite savannas of North America (McPherson 1997) interspecific competition (between species) is as likely as intraspecific competition (within species).

Evidence of competition between savanna trees has been largely inferential (Penridge and Walker 1986, Kenkel 1988, Martens et al. 1997), but has indicated that competition increases with increasing tree density. Tree distribution in savannas can be an indicator of both inter- and intraspecific competition (Martens et al. 1997). Where clumped tree distributions occurs, facilitation is implied at the clump scale with intra-specific competition operating at a larger scale between clumps or individual trees (Martens et al. 1997). With increasing tree density, the effects of intraspecific competition would be expected to result in changes in spatial distribution due to death of individuals (Pielou 1960, Yoda et al. 1963, Mohler et al. 1978), or by decrease in individual size (Mohler et al. 1978). Removal experiments in shrublands have shown that intraspecific competition may or may not occur, depending on resource availability and species rooting patterns (Manning and Barbour 1988, McPherson and Wright 1989, Miller and Huenneke 2000). In monocultures, experimental manipulations have demonstrated that remaining trees may benefit from the removal of conspecific neighbors (Ford 1975) and greenhouse experiments with *P. glandulosa* seedlings have demonstrated marked density-dependent effects on various growth metrics (Van Auken and Bush 1987). Under manipulated field conditions, Ansley et al. (1998) demonstrated intraspecific competition as indicated by differences in adult *P. glandulosa* growth characteristics and water use over several years in contrasting stand densities.

The characteristics of the soil environment may mediate density-dependent competitive interactions. On shallower soils, roots may be concentrated in a smaller soil volume which could increase competition intensity. Research in north Texas savannas has demonstrated that intraspecific competition may be significant on some sites, for example on shallow soils, but not others (Thomas and Sosebee 1978, Nilsen et al. 1984, Ansley et al. 1990, Ansley et al. 1991, Cuomo et al. 1992). This would be due to both the increased reliance by *P. glandulosa* on shallow lateral roots for moisture acquisition, and compression of the available soil volume (Ansley et al. 1990, Ansley et al. 1991, Ansley et al. 1992b, Cuomo et al. 1992). Ansley et al. (1998) demonstrated that intraspecific competition reduced growth and leaf area of *P. glandulosa*, but not transpiration or photosynthetic rates per leaf. Reliance on near-surface, lateral roots that may extend well beyond the plant's canopy may result in competitive interactions whose intensity varies with distance. Evidence from other studies suggests that there may be a further interaction with woody plant density (Smith and Grant 1986, Van Auken and Bush 1987). I might therefore envisage an increasing intraspecific competitive effect where soils are shallow and tree densities are greater. However, Ansley et al. (2001) show a linear increase in *P glandulosa* over 30 years between 0 and 50% aerial cover at this location on Tillman soils. This suggests no density dependence within this range of *P glandulosa* abundance.

Hypotheses

The primary objective of this study was to detect evidence for intraspecific competition of *P. glandulosa* and the relative importance of the relationship with soil depth, and tree stand density. If intraspecific competition is occurring:

H1 - Growth of *P. glandulosa* on deep soils will be greater than that on shallow soils.

H2 - The response of *P. glandulosa* to conspecific neighbor removal will be greater on shallow soils relative to deeper soils.

The second objective was to examine the effect of stand basal area (BA) on the growth of *P. glandulosa* plants.

H3 - For a given soil depth, growth of *P. glandulosa* plants will be inversely proportional to stand BA.

H4 - *P. glandulosa* growth following removal of neighbors will be directly proportional to initial stand BA.

Finally, some measure of tree rooting distances was desirable to estimate the region of belowground influence around each individual tree.

This investigation required a series of removal (thinning) experiments on contrasting soil depths within a range of stand basal areas. Mainly widely spaced, isolated, individual trees characterized study sites. For the purpose of this study therefore, shading effects were not considered.

METHODS

Experimental assessments of intraspecific interactions

Within a stand of single and multi-stemmed *P. glandulosa* trees at both shallow (tree height 2-3 m) and deep soil (tree height 3-4.5 m) sites, 20 individuals separated by a minimum of 25-m were randomly selected for monitoring. Multi-stemmed target trees were subjectively designated as individuals when stems arising from the ground were > 0.5-m apart with no obvious sub-surface connection. The density and size of stems in the vicinity of target plants was quantified by measuring basal area of all *P. glandulosa* stems with a basal diameter ≥ 2-cm within a 10-m radius of target plants. Target trees on each soil were then randomly assigned to a control (n = 10) or neighbor

removal (n = 10) treatment. Control stands remained intact. In neighbor removal stands, all *P. glandulosa* individuals within a 10-m radius about the target were felled in December 1997, and their stumps treated with diesel fuel to minimize vegetative regeneration. Hand applications of a glyphosate spray (Roundup®) were applied as needed during the study period to kill stump resprouts. To experimentally assess growth response to treatment, target trees were measured for basal area growth with dendrometer bands (Palmer and Ogden 1983) and terminal annual shoot length (n = eight shoots/tree randomly selected from canopy perimeter) at the end of the growing season (December 1998 and 1999). If the target tree was multi-stemmed the basal area of the three largest stems was measured. Both absolute ($cm^{2} \cdot yr^{-1}$) and relative ($cm^{2} \cdot cm^{-2} \cdot yr^{-1}$) basal growth rates were calculated. ANOVA and repeated measures ANOVA using NCSS (Hintze 2001), were used to compare tree growth rates. Tukey's multiple comparison test (alpha ≤ 0.05) was used throughout to compare means, and density dependence was assessed with regression analysis, and comparison of regression slopes (Zar 1999).

In a companion investigation, the horizontal sphere of influence or belowground 'ecological field' (Walker et al. 1989) of *P. glandulosa* plants was estimated by injecting the broad-spectrum herbicide hexazinone (Velpar-L®), an effective ground-applied herbicide *for P. glandulosa* (Anonymous 1998, Duncan and McDaniel 2000) into the upper 25 cm of the soil profile. The status of *P. glandulosa* trees was subsequently monitored as a function of distance from the injection points. Herbicide injections were made in *P. glandulosa* stands on both deep (n = 3) and shallow (n = 3) soil sites away from those used in the selective removal experiment. To maximize the probability that shallow lateral roots of *P. glandulosa* plants would be affected, hexazinone injections were made along a pair of intersecting perpendicular 1-m lines. Holes (1-cm diameter; 25-cm deep) cored at 10-cm intervals along each line received 20 ml of hexazinone (25% dilution) in May 1999. Six weeks later all trees within a 15-m radius of the

injection cross were inspected for canopy dieback. Canopy diameters of symptomatic and asymptomatic trees were recorded, as well as a visual estimation of percentage canopy affected. The hexazinone-impacted tree limbs typically experienced a near 100% loss of leaflets, but retained the leaf petiole, giving these limbs a characteristic appearance. ANOVA was used to test for differences in mean distance to impacted trees, mean maximum distance to impacted trees, and the proportion of tree canopy affected on deep and shallow soil sites. Except where indicated statistical significance indicates alpha ≤ 0.05.

RESULTS

Rainfall

Rainfall in 1998 (504 and 427 mm on deep and shallow sites, respectively) was lower than that received in 1999 (560 and 614 mm) and both years were below the long-term average (665 mm) on both sites (Fig. 1, page 10). Monthly rainfall patterns were slightly different between deep and shallow soil sites. In 1998 the shallow soil site received no measurable rainfall from July through September, while the deep soil site received ca. 49 mm. Conversely, the shallow soil site received more rainfall than the deeper soil in spring and late summer in 1999 (Fig. 1).

Response to neighbor removal

Initial basal areas of target *P. glandulosa plants* ranged from 66 to 329 cm^2 (mean ± SE = 153 ± 16 cm^2) on the deep soil sites and 49 to 241 cm^2 (mean ± SE = 85 ± 9 cm^2) on the shallow soil sites. Initial stem size affected basal area growth of *P. glandulosa* only on deep soils and only in 1998; and in that instance, initial size accounted for 19% of the variation in basal area growth (Table 16). However, for this reason relative growth rates (basal area growth (cm^2) per initial basal area (cm^{-2}) per year (yr^{-1}), rather than absolute growth rates are presented.

Table 16. Regression model statistics assessing the relationship of absolute stem growth with initial stem basal area at deep and shallow soils.

Source	R^2	P
Deep soil 1998	0.194	0.05
Deep soil 1999	0.095	n.s.
Shallow soil 1998	0.050	n.s.
Shallow soil 1999	0.190	n.s.

Table 17. Repeated-measures ANOVA model statistics assessing effects of soil depth (deep vs. shallow), presence or absence of neighbors (±) and their interaction on relative, annual basal growth of *P. glandulosa* target trees after the 1998 and 1999 growing season.

Source	d.f.	F value	P
Neighbors ±	1	0.35	n.s.
Soil depth	1	21.33	0.0001
Neighbors ± * soil depth	1	0.07	n.s.
Year	1	6.04	n.s.
Neighbors ± * year	1	10.47	0.01
Soil depth * year	1	18.20	0.001
Neighbors ± * soil depth * year	1	1.01	n.s.

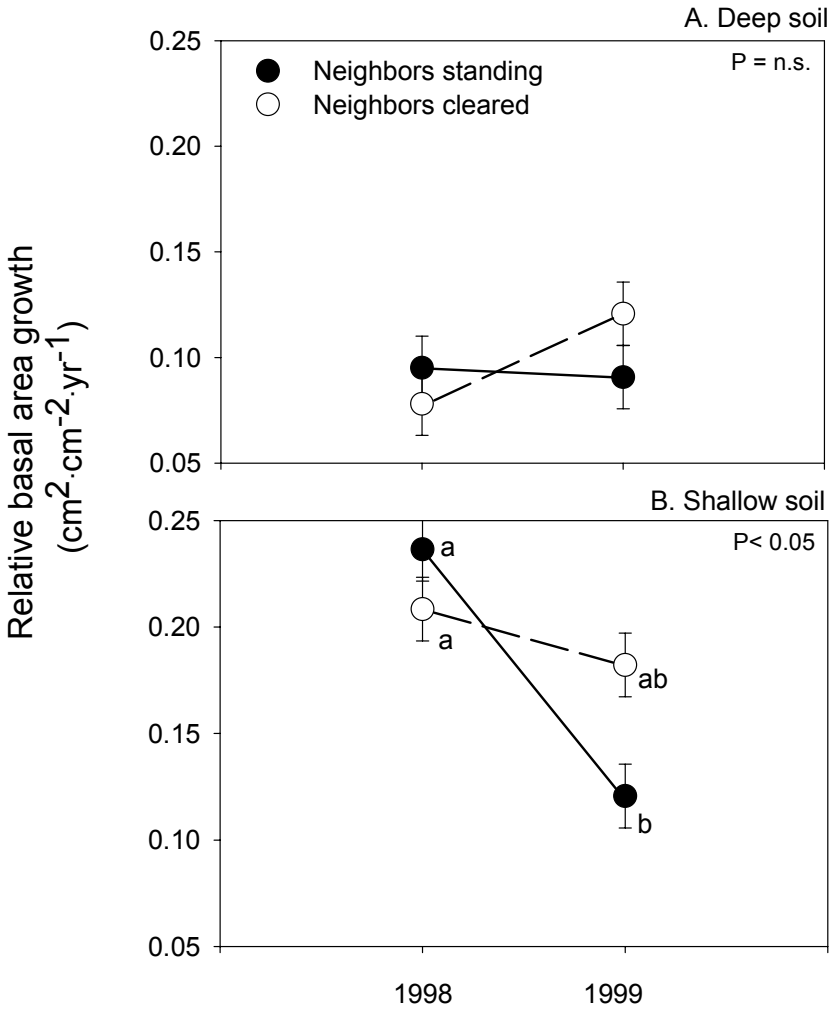

Fig. 18. Relationship between mean (± S.E.) of relative annual basal growth of *P. glandulosa* plants with (standing) and without neighbors (cleared).

Analyses based on relative basal growth generated within-site (soil depth) indicated significant soil depth, soil depth x year, and neighbor x year interactions (Table 17). However, relative basal growth of plants on the deep soils were about half that of plants on shallow soils (Fig. 18). Data are pooled across stands whose mean stem basal area densities ranged from 3.08 $m^2 \cdot ha^{-1}$ on deep soils and 1.5 $m^2 \cdot ha^{-1}$ on the shallow soil site. Mean terminal shoot production was also comparable among *P. glandulosa* plants, regardless of thinning treatment or soil depth (Table 18, Fig. 19).

Density dependent effects on growth

The hypothesis that tree growth in response to soil depth or neighbor removal is a function of stand BA was tested with regression analysis. It was hypothesized that in intact stands (controls), growth of target trees would decrease with increasing stand BA. Conversely, for removal treatments, growth of target trees in low BA stands would be minimally affected by neighbor removal, whereas growth of trees in high BA stands would be strongly affected.

Relative basal area growth of trees on deep soils revealed significant density-dependent growth in 1998 (R^2 = 0.56, $P < 0.05$; Fig. 20C) but not in 1999 (Fig. 20D). There was no evidence of density-dependent effects on growth on the shallow soil in either year (Fig. 21C & D) and slopes of regression lines were statistically comparable on both shallow (t = 0.382) and deep (t = 0.414) soils. *P. glandulosa* response to neighbor removal did not vary with stand BA on either the deep or the shallow soil site (Fig. 20A & B, Fig. 21A & B). However, the coefficient of determination (R^2) values were lower for cleared vs. control stands, suggesting a possible diminution of BA effects. This attenuation effect was translated into shoot growth on the shallow soil sites, where the regression slopes of cleared treatment were less than that where neighbors

Table 18. ANOVA model statistics assessing effects of soil depth (deep vs. shallow), presence or absence of neighbors (±) and their interaction on the stem length of *P. glandulosa* target trees after the 1999 growing season

Source	d.f.	F value	P
Soil depth	1	0.14	n.s.
Neighbors ±	1	0.29	n.s.
Soil depth * neighbors ±	1	1.16	n.s.

Table 19. Summary of ANOVA model statistics for the measures of effect ground- injected herbicide on neighboring *P. glandulosa* trees within 15 m.

Source	Deep soil	Shallow soil	F value	P
Mean distance (m)	11.86	9.82	1.02	n.s.
Mean maximum distance (m)	7.46	12.23	8.25	0.05
Proportion of canopy affected (%)	14.7	29.2	1.54	n.s.

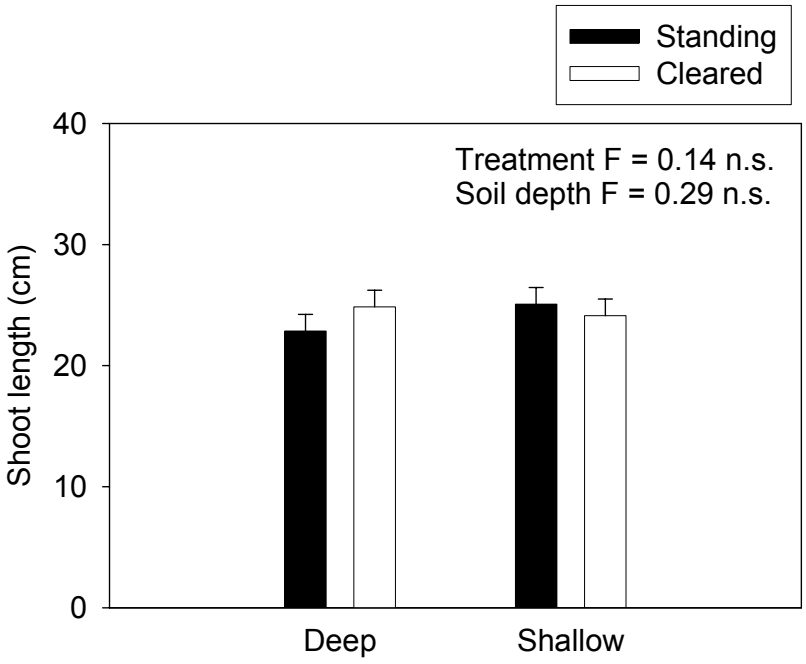

Fig. 19. Relationship of mean (± S.E.) length of terminal shoots (cm) of individual *P. glandulosa* plants to soil depth and presence (standing) and absence (cleared) of neighbors during 1999.

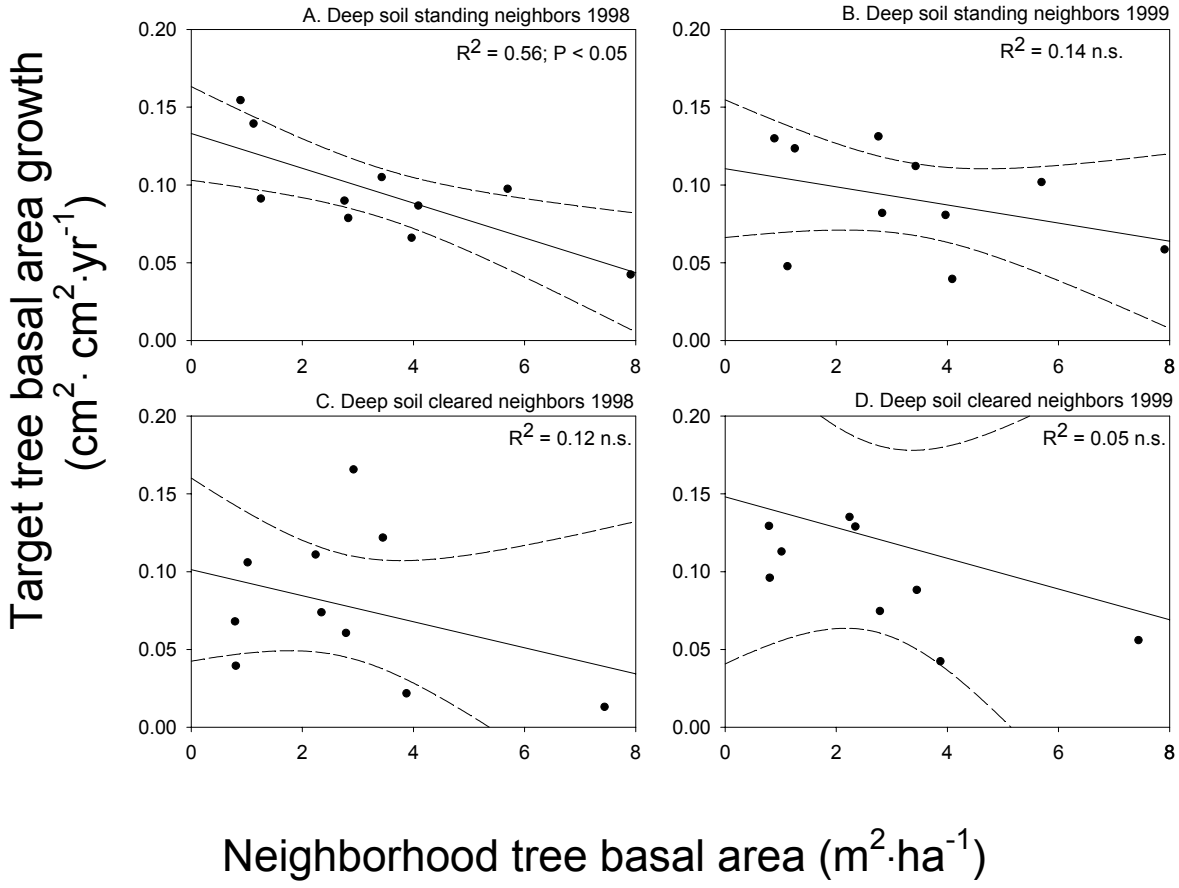

Fig. 20. Relative basal growth of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on deep soil sites at end of 1998 and 1999 season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand.

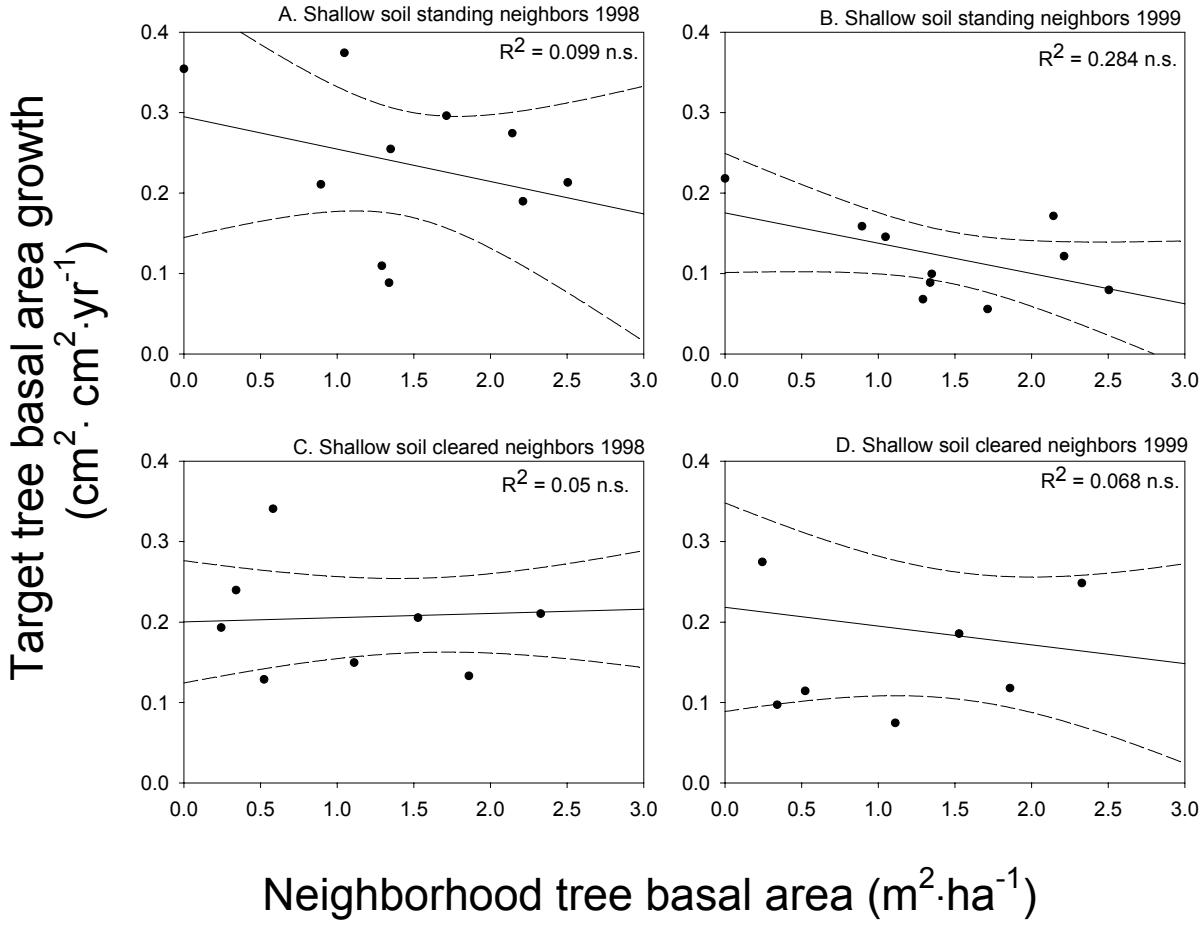

Fig. 21. Relative basal growth of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on shallow soil sites at end of 1998 and 1999 season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand.

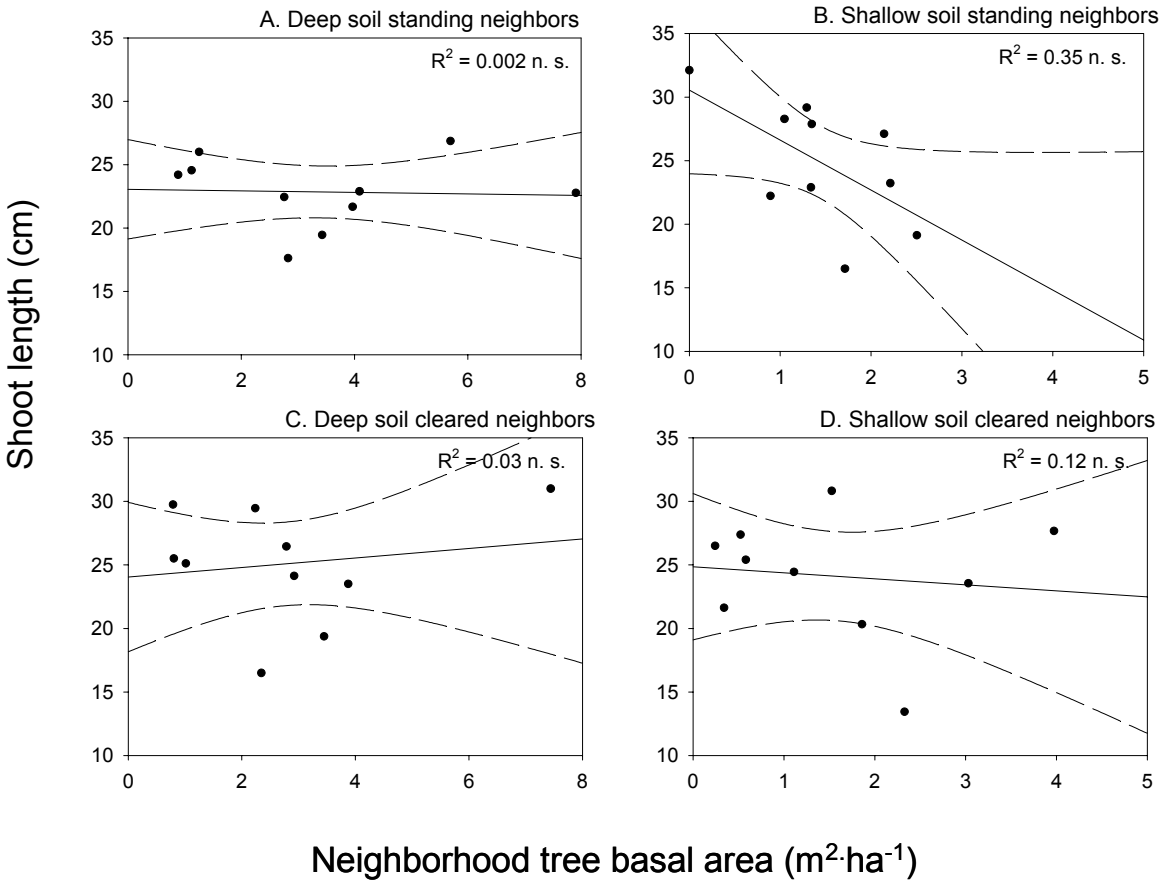

Fig. 22. Length of terminal shoots (cm) of individual *P. glandulosa* plants as a function of pretreatment neighborhood basal area within a 15-m radius on cleared vs. control treatments on deep (A, C) and shallow (B, D) soil sites at end of 1999 growing season. Dashed lines indicate 95% confidence limits. Basal areas for cleared sites (C & D) are those of pretreatment neighboring trees removed from the stand.

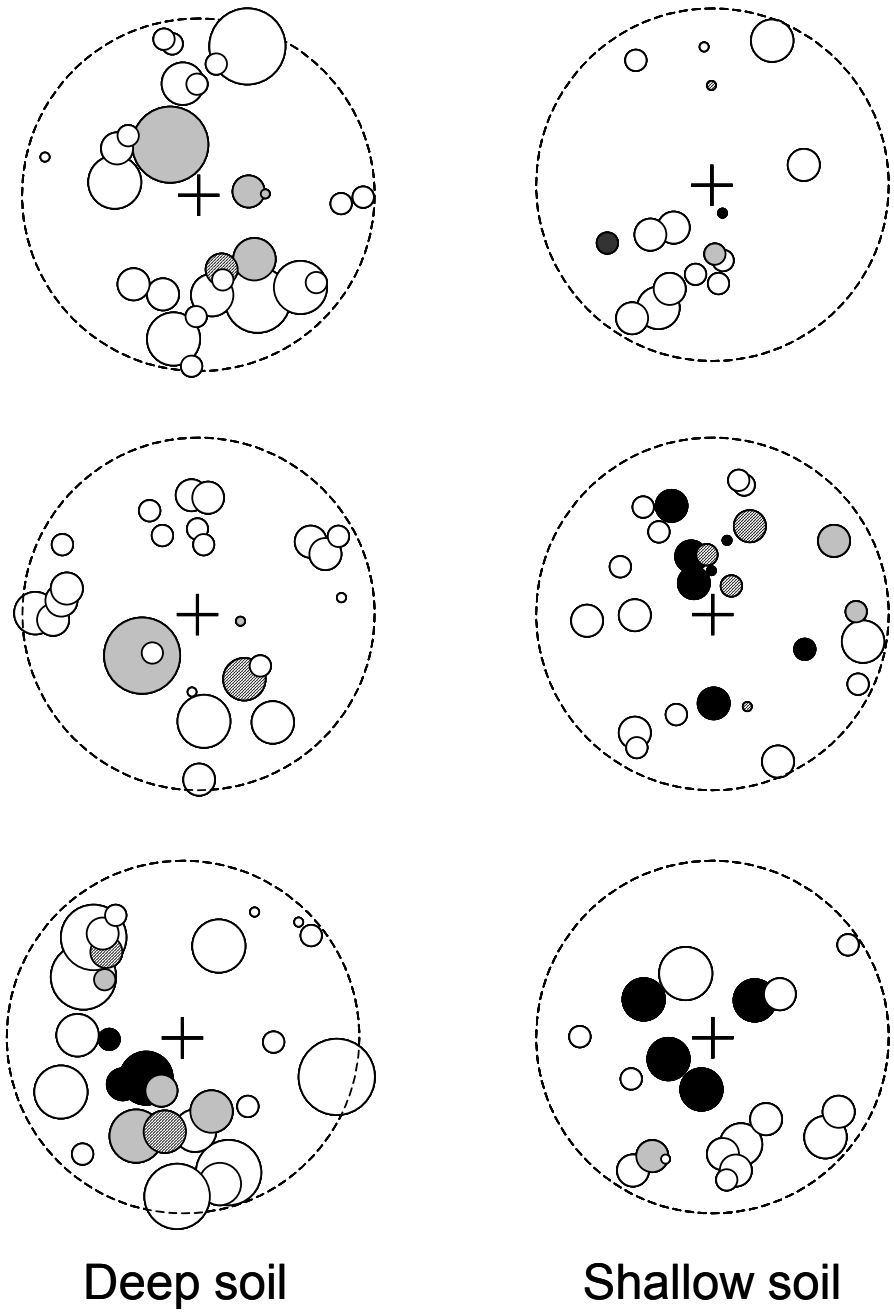

Fig. 23. Response of individual *P. glandulosa* canopies to herbicide injection at points along 1-m perpendicular lines (+). Circles represent locations of *P. glandulosa* canopies in relation to '+' (to scale). Empty circle = no canopy effect; gray fill = 0-33% canopy dieback; hatched fill = 34-66% dieback; solid fill = 67-100% canopy dieback. Dotted line circumscribes area within 15 m of '+'.

were intact ($t = 3.03$ $P < 0.05$) but not deep soil site ($t = 1.06$; n.s., Fig. 21). Target plant shoot growth in response to neighbor removal on shallow and deep soil sites was minimal, regardless of whether target plants were in low or high BA stands (Fig. 22 A & B). Similarly, shoot growth of target plants in control stands was statistically similar in low and high BA stands, though there was a hint of a negative correlation ($R^2 = 0.35$; $P = 0.07$) on the deep soil site (Fig. 22).

Ecological field assessment

Hexazinone-induced leaf fall in P. glandulosa plants within 15 m of an injection site was more pronounced on shallow soils (33.8% of plants showing some effect) than on deep soils (13.2% of plants showing some effect) (Fig. 23). Furthermore, each of the three stands on the shallow site had plants experiencing 67-100% canopy dieback, whereas this level of dieback occurred in only one of three stands on the deep soils. Mean maximum distance values also indicated that trees on shallow soils were more likely to be affected and at a greater distance from source (Table 19).

DISCUSSION

Evidence for density dependent regulation of growth in *P. glandulosa* stands was generally weak. However, trends from the relationship of growth rates with neighborhood thinning indicate a deterioration of this relationship following removal of stems where stem density is high (Fig. 21 & 22). Indications of competition from grass-tree studies where *P. glandulosa* growth following herbaceous sward removal was greater on shallower soils (Chapter III) might suggest that intraspecific responses on shallow soils should be stronger. This is supported by an increase in relative growth rates on shallow soils compared to deep soils following competitive release (Fig. 18). However mean increases in basal growth as a response to clearing were evident at both sites only during 1999. Although 1999 was wetter than 1998, the shallow soil site received more

rainfall in 1999 than the deep soil site (614 vs. 560 mm), thus confounding the interpretation of soil depth vs. rainfall effects

The highest pre-treatment neighborhood basal area densities were on the deep soil site, so the subsequent growth response to clearing could be expected to be stronger. However, at both deep and shallow soil sites a measure of variance of the relationship (R^2 in Fig. 21 and 22) between basal growth and neighborhood stem basal area decreased in response to neighborhood stem thinning. This suggests that intraspecific competition between trees is minimal at both sites and somewhat independent of initial basal area densities.

The restriction of intraspecific competition to immediate neighbors has been demonstrated for pines (Kenkel 1988) and annuals (Mack and Harper 1977). In stressed systems, neighborhood competition assumes that the root architecture must shift from an intensive (laterally symmetrical, e.g. many grasses) architecture around the plant base to an extensive (laterally penetrating regions well beyond the canopy, e.g. desert shrubs) architecture (Larcher 1995). Knowledge of root architecture may therefore be critical in explaining competitive interactions (Manning and Barbour 1988). Evidence in this study from the distribution of canopies exhibiting symptomatic dieback from the shallow herbicide injection suggests that *P. glandulosa* roots are 'foraging' at distances up to 7 to 12 m from their canopies (Table 19). The variable response to the herbicide supports the model of a complex, spatially heterogeneous, lateral root architecture for *P. glandulosa* supporting the findings by Heitschmidt et al. (1988) and Ansley et al. (1990). This suggests that density dependent effects may be difficult to predict and dispersed to a wider community rather than immediate neighbors. This could effectively contribute to the blurring of any response of individual trees to the thinning of immediate neighbors, and a treatment area (greater than 10 m) may encourage a more significant response from the target tree. Nonetheless, the greater foraging distance of lateral roots on the shallow soil site combined with the indication of a greater positive growth

response of trees experiencing neighborhood clearing, supports the model of higher allocation of resources to lateral roots on sites where accessibility to deeper moisture may be limited (Heitschmidt et al. 1988, Ludwig 1977, Ansley et al. 1990, Cuomo et al. 1992).

In summary, these data indicate only weak trends of intraspecific competition of *P. glandulosa* similar to findings by Ansley et al. (2001). Although *P. glandulosa* may produce an extensive near-surface lateral root network particularly on shallow soils, these roots may be only used opportunistically and the tree may not necessarily depend on them. During a normal or above-normal rainfall year however, the magnitude of the interactions examined in this study may increase. Furthermore, the Rolling Plains have only relatively recently experienced woody invasion of *P. glandulosa.* Most trees are only decades old or less, and self-thinning or self-regulation of *P. glandulosa,* while negligible under the conditions of this study, may intensify as plants increase in size.

CHAPTER VI

SUMMARY AND CONCLUSIONS

TREE ON GRASS EFFECT

Previous savanna research has paid more attention to the effect of the presence of trees on the grass layer than the reverse relationship (grass on tree) and interactions between trees themselves (tree on tree). This study addressed this discrepancy by experimental manipulations that attempted to tease out these different mechanistic components.

The presence of individual trees in savannas has been demonstrated to have positive, negative, and neutral effects on grasses. Although most treatments demonstrated neutral (neither competition or facilitation) responses, the removal of tree-root competition (Chapter III) showed a marked increase in herbaceous production, and no evidence for competition aboveground. Although tree density has been shown to adversely affect herbaceous production, there has been speculation about the underlying cause (Scifres and Polk 1974). These data suggest that below- rather than aboveground competition is responsible. Other studies have demonstrated that herbaceous productivity may be elevated at certain tree densities due to modification of conditions above- and belowground in the sub-canopy environment (Heitschmidt et al. 1986). However, generally, there was no apparent benefit to understorey plants in subcanopy sites with or without the presence of the canopy itself. Given that *P. glandulosa* tree roots may extend several times the tree canopy diameter (Heitschmidt et al. 1988, Chapter V) this effect may extend well beyond the canopy, affecting herbaceous productivity at the landscape scale.

The growth of perennial native grasses may have been inhibited by the presence of invasive annual grasses. These exotic species (*Bromus* spp.) are known to be very competitive, albeit for only short periods in the spring, and may have opportunistically sequestered any elevated soil nutrients while suppressing

growth of native grasses. Contributing little dry biomass to total herbaceous production, the presence of exotic grasses may have masked the response in the natives (Haferkamp et al. 1995, Haferkamp et al. 1998). The significance of the role of these annual grasses and their competitive effect on the grass and tree component requires further investigation.

The lack of any further evidence for facilitation due to the tree canopy may have been because any beneficial shading effect may have been countered by interception of precipitation by the canopy in what were drier than normal years. This implies that during dry years when precipitation events are small (which are not uncommon in north Texas) individual *P. glandulosa* trees may have a several competitive advantages; through their ability to access deeper water, to compete directly with grasses through an extensive lateral root system, and by channeling canopy-intercepted rainfall via stem-flow.

The dry conditions, particularly in the summer, during both years resulted in little or even negative growth of warm season grasses, precluding a comparison of tree-grass effects with their cool-season counterparts. However, this does highlight the direct effect of annual climate fluctuation on savanna dynamics on the herbaceous layer. Different annual climate patterns favoring one physiologically distinct group of plants over another may contribute to interacting mechanisms which facilitate coexistence of all groups over the long-term.

GRASS ON TREE EFFECT

It has been demonstrated that coexistence of trees with grasses in savannas may be due to the ability of woody plants to gain access to resources below the reach of most grasses and forbs. However, where accessible soil volume decreases, competition between these two physiognomic groups should intensify. These data demonstrate that given adequate precipitation, grass-tree competition for water and nutrients (P) becomes increasingly important with

decreasing soil depth. This has implications for a savanna models that attempt to explain tree-grass coexistence by belowground resource partitioning (Walter 1971). This phenomenon is probably system specific, where the interplay of soils and climate and belowground root architecture governs savanna dynamics. Although the moderate mowing regime did not enhance tree growth (Stuart-Hill and Tainton 1989), the effect of complete sward removal suggest that higher mowing rates or increasing grazing pressure could decrease grass-tree competition and enhance tree growth rate. The role of the grass effect on tree in savannas may have been underestimated, and raises the question: can a healthy grass sward slow the rate of woody encroachment into savannas and grasslands?

Fire has been considered to be a key mechanism in the dynamics of savannas, by controlling establishment of woody species and facilitating grass and forb establishment and survival (Hochberg et al. 1994). Surviving adult trees can benefit from the post-fire nutrient release and relaxation of grass-tree competition (Chapter IV). The reason why this post-fire benefit was demonstrated only on deeper soils is unknown but may be related to nutrient mobilization where available water was limited.

TREE ON TREE EFFECT

Although savanna tree densities vary considerably, it can be envisaged that at high densities there may some degree of competitive self-regulation. These data did not demonstrate any strong indications of density dependent growth, but this may have been due to low rainfall. The extensive lateral root network produced by *P. glandulosa*, extending well beyond the canopy (Heitschmidt et al. 1988, Chapter V), may have blurred any response of surviving tree to removal of trees in the immediate (10-m radius) neighborhood.

Alternatively, the lateral root network may be used only opportunistically and the tree may be decoupled from competitive interactions near the soil

surface. These data and those from Chapters III & IV suggest that intraspecific competition is more likely in neighborhoods of high basal area, and on shallower soils. This savanna is also relatively young (<150 years) and stand densities are likely to increase and intensify intraspecific competition.

DIRECTIONS FOR FUTURE RESEARCH

The unusually dry climatic conditions during the two years of study probably had a marked effect on the outcome of all the experiments. The most significant responses occurred in 1999 when precipitation although below normal, was more substantial. Furthermore, the climate may have been responsible for the absence of other tree-grass interactions demonstrated in previous studies. It would be prudent to withhold conclusions about all the non-competitive interactions until similar studies were conducted during both normal and wetter years.

Competitive interactions may have minimum and maximum resource requirements to be exhibited (Callaway 1997). When rainfall is limited, the productivity of all plants within a given community may be reduced enough to make competitive response negligible (e.g. Knoop and Walker 1985). A series of similar studies repeated in wet, normal, and dry years, and ideally over a longer time period, would help quantify these operating limits to establish what competitive and facilitative interactions contribute to savanna dynamics over the long-term.

REFERENCES

Amiotti, N. M., P. Zalba, L. F. Sanchez, and N. Peinemann. 2000. The impact of single trees on properties of loess-derived grassland soils in Argentina. Ecology **81**:3283-3290.

Anonymous. 1998. Velpar L. H-63377. Du Pont de Nemours and Company.

Ansley, R. J., and P. W. Jacoby. 1998. Manipulation of fire intensity to achieve mesquite management goals in north Texas. *in* T. L. Pruden and L. A. Brennan, editors. Tall Timbers Fire Ecology Conference No 20, Tallahassee, Florida, U.S.A.

Ansley, R. J., P. W. Jacoby, and G. J. Cuomo. 1990. Water relations of honey mesquite following severing of lateral roots: influence of location and amount of subsurface water. Journal of Range Management **43**:436-442.

Ansley, R. J., P. W. Jacoby, and R. A. Hicks. 1991. Leaf and whole plant transpiration in honey mesquite following severing of lateral roots. Journal of Range Management **44**:577-583.\

Ansley, R. J., P. W. Jacoby, D. R. Lucia, and D. Jones. 1994. Effect of summer and winter fires and fire frequency on honey mesquite mortality. Abstract *in* Proceedings. Society for Range Management, 47th Annual Meeting, Colorado Springs, CO.

Ansley, R. J., P. W. Jacoby, C. H. Meadors, and B. K. Lawrence. 1992a. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). Journal of Arid Environments **22**:147-159.

Ansley, R. J., B. A. Kramp, and T. R. More. 1995. Development and management of mesquite savanna using low intensity prescribed fires. Pages 155-161 *in* Fire Effects on Rare and Endangered Species and Habitat Conference. IAWF, Coeur d'Alene, Idaho, U.S.A.

Ansley, R. J., D. L. Price, S. L. Dowhower, and D. H. Carlson. 1992b. Seasonal trends in leaf area of honey mesquite trees: Determination using image analysis. Journal of Range Management **45**:339-344.

Archer, S. R. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. Pages 13-68 *in* M. Vavra, W. Laycock, and R. Pieper, editors. Ecological Implications of Livestock Herbivory in the West. Society for Range Management, Denver, CO, U.S.A.

Archer, S. R. 1995a. Herbivore mediation of grass-woody plant interactions. Tropical Grasslands **29**:218-235.

Archer, S. R. 1995b. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience **2**:83-99.

Archer, S. R., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: Biogeochemical consequences of woody plant expansion. *in* E.-D. Schulze, D. Schimel, I. C. Prentice, M. Heimann, S. Harrison, E. Holland, and J. Lloyd, editors. Global Biogeochemical Cycles in the Climate System. Academic Press.

Archer, S. R., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs **58**:111-127.

Asner, G., S. R. Archer, R. Hughes, R. Ansley, and C. Wessman. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937-1999. Global Biogeochemical Cycles **9**:1-20.

Baldwin, V. C., K. D. Peterson, A. C. III, R. B. Ferguson, M. R. Strub, and D. R. Bower. 2000. The effects of spacing and thinning on stand and tree characteristics of 38-year-old Loblolly Pine. Forest Ecology and Management **137**:91-102.

Ballaré, C. L., and J. J. Casal. 2000. Light signals perceived by crop and weed plants. Field Crops Research **67**:149-160.

Barnes, P. W., and S. R. Archer. 1999. Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? Journal of Vegetation Science **10**:525-536.

Bedunah, D. J., and R. E. Sosebee. 1986. Influence of mesquite control on soil erosion on a depleted range site. Journal of Soil and Water Conservation **41**:131-135.

Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology **75**:922-932.

Belsky, A. J., and C. D. Canham. 1994. Forest gaps and isolated savanna trees: an application of patch dynamics in two ecosystems. Bioscience **44**:77-84.

Bomar,.G. W. 1983. Texas Weather. University of Texas Press, Austin, U.S.A.

Bond, W. J., and B. van Wilgen. 1996. Fire and Plants. Chapman and Hall, New York, NY, U.S.A.

Breshears, D. D., P. M. Rich, F. J. Barnes, and K. Campbell. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications **7**:1201-1215.

Brown, J. R., and S. R. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia **80**: 19-26.

Brown, J. R., and S. R. Archer. 1990. Water relations of a perennial grass and seedling versus adult woody plants in a subtropical savanna, Texas. Oikos **57**:366-374.

Callaway, R. M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia **112**:143-149.

Chapin, F. S., III. 1991. Integrated responses of plants to stress: a centralized system of physiological responses. Bioscience **41**:29-36.

Christensen, N. L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia **31**:27-44.

Christensen, N. L., and C. H. Muller. 1975. Effect of fire on factors controlling plant growth in *Adenostoma* chaparral. Ecological Monographs **45**:29-55.

Clayton, L. 1993. Historic Ranches of Texas. University of Texas, Austin, U.S.A.

Covington, W. W., and S. S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients on woody debris and forest floor. Forest Science **30**:183-192.

Cuomo, C. J., R. J. Ansley, P. B. Jacoby, and R. E. Sosebee. 1992. Honey mesquite transpiration along a vertical site gradient. Journal of Range Management **45**:334-338.

Dahl, B. E., R. E. Sosebee, J. P. Goen, and C. S. Brumley. 1978. Will mesquite control with 2,4,5-T enhance grass production? Journal Range Management **31**:129-131.

Daigal, J. J. 1978. Descriptive legend for the soil survey of the 9-mile research site of the Texas Agricultural Experiment Station, Vernon, Texas.

Dawson, T. E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant relations. Oecologia **95**:565-574.

Dawson, T. E., and J. S. Pate. 1996. Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia **107**:13-20.

de Ronde, C., J. G. Goldammer, D. D. Wade, and R. V. Soares. 1990. Prescribed fire in industrial pine plantations. Pages 216-265 *in* J. G. Goldammer, editor. Fire in the Tropical Biota. Springer-Verlag, New York, U.S.A.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology **72**: 1066-1088.

Dumontet, S., H. Dinel, A. Scopa, A. Mazzatura, and A. Saracino. 1996. Post-fire soil microbial biomass and nutrient content of a pine forest soil from a dunal Mediterranean environment. Soil Biology and Biochemistry **28**:1467-1475.

Duncan, K., and K. McDaniel. 2000. Mesquite Control: Individual Treatments. College of Agriculture and Home Economics, New Mexico State University.

Duncan, R. P. 1991. Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecology **79**:1073-1084.

Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia **88**:430-434.

Fisher, C. E. 1950. The mesquite problem in the southwest. Journal of Range Management **3**:60-70.

Fisher, R. F. 1990. Amelioration of soils by trees. Pages 290-300 *in* S. Gessel, editor. Sustained Productivity of Forest Soils. Faculty of forestry, University of British Columbia, Vancouver, Canada.

Fisher, R. F. 1995. Amelioration of degraded rain forest soils by plantations of native trees. Soil Science Society of America Journal **59**:544-549.

Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. Journal of Ecology **63**: 311-333.

Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American southwest. Climatic Change **17**:305-330.

Haase, S. M., and S. S. Sackett. 1996. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Pages 459 *in* T. L. Pruden and L. A. Brennan, editors. 20th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Boise, Idaho, U.S.A.

Hach Company. 1998. Analytical Procedures of DR/2000 and DR/3000 Instruments. Loveland, CO, U.S.A.

Haferkamp, M. R., D. Palmquist, D. Young, and M. D. MacNeil. 1995. Influence of temperature on germination of Japanese brome seed. Journal of Range Management **48**:264-266.

Haferkamp, M. R., R. K. Heidtschmidt, and M. G. Karl. 1998. Clipping and Japanese brome reduce western wheatgrass standing crop. Journal of Range Management **51**:692-698.

Haworth, K., and G. R. McPherson. 1995. Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semi-arid savanna. Journal of Arid Environments **31**:153-170.

Heitschmidt, R. K., R. J. Ansley, S. L. Dowhower, P. W. Jacoby, and D. L. Price. 1988. Some observations from the excavations of honey mesquite root systems. Journal of Range Management **41**:226-231.

Heitschmidt, R. K., and S. L. Dowhower. 1991. Herbage response following control of honey mesquite within single tree lysimeters. Journal of Range Management **44**:144-149.

Heitschmidt, R. K., R. D. Schultz, and C. J. Scifres. 1986. Herbaceous biomass dynamics and net primary production following chemical control of honey mesquite. Journal of Range Management **39**:67-71.

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology **88**:213-229.

Hintze, J. L. 2001. Number Cruncher Statistical Systems 2001 User's Guide. Number Cruncher Statistical Systems. Kaysville, Utah, U.S.A..

Hobbs, T. N., and D. S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. Journal of Range Management **37**:402-405.

Hochberg, M. E., J. C. Menaut, and J. Gignoux. 1994. The influences of tree biology and fire in the spatial structure of the West African savannah. Journal of Ecology **82**:217-226.

Hodgkinson, K. C. 1998. Sprouting success of shrubs after fire: height dependent relationships for different strategies. Oecologia **115**:64-72.

House, J., S. R. Archer, D. Breshears, and R.J. Scholes. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeogrphy **30**:1-15.

Isichei, A. O., and J. I. Muoghalu. 1992. The effects of tree canopy cover on soil fertility in a Nigerian savanna. Journal of Tropical Ecology **8**:329-338.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. V. Rooyen. 1996. Tree spacing and coexistence in semiarid savannas. Journal of Ecology **84**:583-595.

Jensen, M., A. Michaelsen, and M. Gashaw. 2001. Response in plant, soil inorganic and microbial nutrient pools to experimental fire, ash and biomass addition in a woodland savanna. Oecologia.**128**: 85-93

Johnson, R. W., and J. C. Tothill. 1985. Definition and broad geographic outline of savanna lands. Pages 1-13 *in* J. C. Tothill and J. J. Mott, editors. Ecology and Management of the World's Savannas. Australian Academy of Science, Canberra, Australia.

Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. Journal of Ecology **82**:519-531.

Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology **69**:1017-1024.

Keppel, G. 1991. Design and Analysis: A Researcher's Handbook, Prentice-Hall.

Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. Journal of Ecology **73**:235-253.

Krebs, C. J. 1999. Ecological Methodology, 2nd edition. Benjamin Cummings, Menlo Park, CA, U.S.A.

Larcher, W. 1995. Physiological Plant Ecology, 3rd edition. Springer-Verlag, Berlin, Germany.

Larkin, T. J., and G. W. Bomar. 1983. Climatic Atlas of Texas. Texas Department of Water Resources. Austin, TX.

Laxson, J. D., W. H. Schacht, and M. K. Owens. 1997. Above-ground biomass yields at different densities of honey mesquite. Journal of Range Management **50**:550-554.

Lee, D. W. 1985. Duplicating foliage shade for research on plant development. Hortscience **20**.

Ludwig, J. A. 1977. Distributional adaptions of root systems in desert environments. Pages 85-91 *in* J. K. Marshall, editor. The Below Ground Ecosystem: A Synthesis of Plant Associated Processes. Range Science Department, series 26, Fort Collins, CO. Colorado State University, U.S.A.

Mack, R. N., and J. L. Harper. 1977. Interference in dune annuals: Spatial pattern and neighborhood effects. Journal of Ecology **65**:345-363.

MacLean, D. A., Woodley, S. J. Weber, M. G. and R. W. Wein. 1983. Fire and nutrient cycling. Pages 11-132 *in* The Role of Fire in Northern Circumpolar Ecosystems, R.W. Wein and D.A. MacLean. SCOPE. Wiley and Sons, New York, U.S.A.

Madany, M. H., and N. E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology **64**:661-667.

Manning, S. J., and M. G. Barbour. 1988. Root systems, spatial patterns, and competition for soil moisture between two desert subshrubs. American Journal of Botany **75**:885-893.

Martens, S. N., D. D. Breshears, C. W. Meyer, and F. J. Barnes. 1997. Scales of above-ground and below-ground competition in a semi-arid woodland detected from spatial pattern. Journal of Vegetation Science **8**:655-664.

McDaniel, K. C., J. H. Brock, and R. H. Haas. 1982. Changes in vegetation and grazing capacity following honey mesquite control. Journal Range Management **35**:551-557.

McKee, W. H. 1982. Changes in soil fertility following prescribed burning on coastal plain pine sites. Forest Research Paper SE-234, USDA.

McPherson, G. R. 1992. Comparison of linear and non-linear overstory-understory models for ponderosa pine: a conceptual framework. Forest Ecology and Management **55**:31-34.

McPherson, G. R. 1997. Ecology and Management of North American Savannas, 1st edition. University of Arizona Press, Tucson, U.S.A.

McPherson, G. R., and H. A. Wright. 1989. Direct effects of competition on individual J*uniperus pinchotii* plants: a field study. Journal of Applied Ecology **26**:979-988.

McPherson, G. R., H. A. Wright, and D. B. Wester. 1988. Patterns of shrub invasion in semiarid Texas grasslands. The American Midland Naturalist **120**:391-397.

Menaut, J. C., J. Gignoux, and C. a. C. Prado, J. 1990. Tree community dynamics in a humid savanna of the Côte-d'Ivoire: modeling the effects of fire and competition with grass and neighbours. Journal of Biogeography **17**: 471-481.

Miller, D., S. R. Archer, S. F. Zitzer, and M. T. Longnecker. 2001. Annual rainfall, topoedaphic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). Journal of Arid Environments **48**:23-33.

Miller, R. E., and L. F. Huenneke. 2000. Demographic variation in a desert shrub, *Larrea tridentata*, in response to a thinning treatment. Journal of Arid Environments **45**:315-323.

Mohler, C. L., P. L. Marks, and D. G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology **66**:599-614.

Mordelet, P., L. Abbadie, and J. C. Menaut. 1993. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Cote d'Ivoire). Plant and Soil **153**:103-111.

National Oceanic and Atmospheric Administration. 2001. Comparative Climatic Data For the United States [1971 - 2000]. National Climate Data Center, Asheville, N.C.

Naumburg, E., L. E. DeWald, and T. E. Kolb. 2001. Shade responses of five grasses native to southwestern U.S. *Pinus ponderosa* forests. Canadian Journal of Botany **79**:1001-1009.

Nilsen, E.T., M. R. Sharifi, P. W. Rundel, 1984. Comparative water relations of phreatophytes in the Sonora Desert of California. Ecology **65**:767-778.

Palmer, J., and J. Ogden. 1983. A dendrometer band study of the seasonal pattern of radial increment in kauri (*Agathis australis*). New Zealand Journal of Botany **21**:121-126.

Patch N. L. and Felker P. 1997. Influence of silvicultural treatments on growth of mature mesquite (*Prosopis glandulosa* var. *glandulosa*) nine years after initiation. Forest Ecology and Management **94**: 37-46.

Pearcy, R. W., J. R. Ehleringer, H. A. Mooney, and P. W. Rundel. 1996. Plant Physiological Ecology. Field Methods and Instrumentation. 1st edition. Chapman and Hall, London, U.K.

Penridge, L. K. and J. Walker. 1986. Effect of neighbouring trees on eucalypt growth in a semi-arid woodland in Australia. Journal of Ecology **74**:925-936.

Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology **48**:575-584.

Reich, P. B. 1983. Effects of low concentrations of 03 on net photosynthesis, dark respiration, and chlorophyll contents in aging hybrid poplar leaves. Plant Physiology **73**:291-296.

Sandland, R. L., J. C. Alexander, and K. P. Haydock. 1982. A statistical assessment of the dry-weight-rank method of pasture sampling. Grass and Forage Science **37**:263-272.

San Jose, J. J., M. R. Farinas, and J. Rosales. 1991. Spatial patterns of trees and structuring factors in a *Trachypogon* savanna of the Orinoco Llanos. Biotropica **23**:114-123.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03. Cary, NC.

Schoch, P., and D. Binkley. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. Forest Ecology and Management **14**:13-22.

Scholes, R. J., and B. H. Walker. 1993. An African Savanna: Synthesis of the Nylsvley Study. Cambridge University Press, Cambridge.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Scifres, C. J., and D. B. J. Polk. 1974. Vegetation response following spraying a light infestation of honey mesquite. Journal of Range Management **27**:462-465.

Scifres, C. J., M. M. Kothmann, and G. W. Mathis. 1974. Range site and grazing system influence regrowth after spraying honey mesquite. Journal of Range Management **27**:97-100.

Scifres, C. J., J. L. Mutz, R. E. Whitson, and D. L. Drawe. 1982. Interrelationships of huisache canopy cover with range forage on the coastal prairie. Journal of Range Management **35**:558-562.

Shainsky, L. J., and S. R. Radosevich. 1992. Mechanisms of competition between Douglas-fir and red alder seedlings. Ecology **73**:30-45.

Skarpe, C. 1992. Dynamics of savanna ecosystems. Journal of Vegetation Science **3**:293-300.

Smith, H. 1975. Phytochrome and Photomorphogenesis. McGraw-Hill Book Company, New York.

Smith, T. M., and K. Grant. 1986. The role of competition in the spacing of trees on a *Burkea africana* - *Terminalia sericea* savanna. Biotropica **18**:219-223.

Soriano, A., Alberto, and O. Sala. 1983. Ecological strategies in a patagonian arid steppe. Vegetatio **56**:9-15.

Stuart-Hill, G. C., and N. M. Tainton. 1989. The competitive interaction between *Acacia karoo* and the herbaceous layer and how this is influenced by defoliation. Journal of Applied Ecology **26**:285-298.

Teague, R., R. Borchardt, J. Ansley, B. Pinchak, J. Cox, J. K. Foy, and J. McGrann. 1997. Sustainable management strategies for mesquite rangeland: The Wagonner Kite project. Rangelands **19**:4-6.

Teague, W. R., and S. L. Dowhower. 2002. Patch dynamics under rotational and continuous grazing management in large, heterogeneous paddocks. Journal of Arid Environments **53**:211-229.

Texas Water Development Board. 2002. Drought in Perspective 1996 -1998. TWDB. Austin, TX.

Thomas, G. W., and R. E. Sosebee. 1978. Water relations of honey mesquite-A facultative phreatophyte. Pages 414-418 *in* D. N. Hyder, editor. Proceedings of the First International Rangeland Congress, Denver, Colorado, U.S.A.

Tiedemann, A. R., and J. O. Klemmedson. 1973. Effect of mesquite on physical and chemical properties of the soil. Journal of Range Management **26**:27-29.

Tiedemann, A. R., and J. O. Klemmedson. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Journal of Range Management **30**:261-267.

Topp, G. C., and J. L. Davis. 1985. Measurement of soil water content using time-domain reflectometry (TDR): A field evaluation. Soil Science Society of America Journal **49**:19-24.

Topp, G. C., J. L. Davies, W. G. Bailey, and W. D. Zebchuk. 1984. The measurement of soil water content using a portable TDR hand probe. Canadian Journal of Soil Science **64**:313-321.

USDA. 1962. Soil Survey of Wilbarger County, Texas. Texas Agricultural Experimental Station and United States Agriculture Department Soil Conservation Service. Washington, D.C.

Valmis, J., and J. D. Gowans. 1961. Availability of nitrogen, phosphorus and sulphur after brush burning. Journal of Range Management **14**:38-40.

Van Auken, O. W., and J. K. Bush. 1987. Influence of plant density on growth of *Prosopis glandulosa* var. *glandulosa* and *Buchlöe dactyloides*. Bulletin Torrey Botanical Club **114**:393-401.

Villagra, G. M. L., and P. Felker. 1997. Influence of understory removal, thinning and P fertilization on N-2 fixation in a mature mesquite (*Prosopis glandulosa* var*. glandulosa*) stand. Journal of Arid Environments **36**:591-610.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556-590 *in* B. J. Huntley and B. H. Walker, editors. Ecology of Tropical Savannas. Springer-Verlag, Berlin, Germany.

Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology **69**:473-498.

Walker, J., P. H. Sharpe, L. Penridge, and H. Wu. 1989. Ecological field theory: the concept and field tests. Vegetatio **83**:81-95.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK.

Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia **112**:156-164.

Whisenant, S. G., and D. W. Uresk. 1990. Spring burning Japanese brome in a western wheatgrass community. Journal of Range Management **43**:205-208.

Yeaton. R. I. 1988. Porcupines, fires and the dynamics of the tree layer of *Burkea africana* savanna. Journal of Ecology **76**: 1017-1029.

Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of Biology **14**: 107-129.

Young, M. D., and O. T. Solbrig. 1993. The World's Savannas: Economic Driving Forces, Ecological Constraints and Policy Options for Sustainable Land Use. Parthenon Publishing Group, Carnforth, U.K.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice-Hall, Inc., Englewood Cliffs, N.J., U.S.A.

Zitzer, S. F., Archer, S. R., and T. W. Boutton. 1996. Spatial variability in the potential for symbiotic N_2 fixation by woody plants in a subtropical savanna ecosystem.

APPENDIX

Table A1. Multiple contrasts for 1998 *N. leucotricha* basal area change, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**P**
	model	9	1.22	0.2992
1	subcanopy v gap	1	3.33	0.0722
2	+above v -above	1	0.17	0.6785
3	+below v -below	1	0.08	0.7786
4	+above +below v -above -below	1	0.03	0.8562
5	+above +below v -above +below	1	2.88	0.0939
6	+above -below v -above -below	1	1.23	0.2710
7	sub +below v -below	1	0.01	0.9228
8	sub +above v -above	1	1.35	0.2486
9	sub +above +below v -above -below	1	0.16	0.6943
10	gap -below v +below	1	0.32	0.5737
11	gap +above v -above	1	0.05	0.8209
12	gap +above +below v -above -below	1	0.31	0.5770
13	sub -below v gap -below	1	2.70	0.1047
14	sub +below v gap +below	1	0.88	0.3515
15	sub -above v gap -above	1	3.86	0.0535
16	sub +above v gap +above	1	0.71	0.4028
17	natural shade v synthetic shade	1	1.19	0.2795
18	natural shade v no shade	1	0.17	0.6784
19	synthetic shade v no shade	1	0.68	0.4122

Table A2. Multiple contrasts for 1998 *N. leucotricha* relative change in tillers/plant tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.00526$) ** ($P < 0.05$ with Bonferroni correction $P < 0.00263$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.00053$).

	Contrast	**d.f.**	**F value**	**P**
	model	9	0.69	0.7156
1	subcanopy v gap	1	0.92	0.3402
2	+above v -above	1	0.00	0.9956
3	+below v -below	1	3.62	0.0610
4	+above +below v -above -below	1	1.93	0.1696
5	+above +below v -above +below	1	0.13	0.7148
6	+above -below v -above -below	1	0.13	0.7206
7	sub +below v -below	1	0.93	0.3394
8	sub +above v -above	1	0.40	0.5268
9	sub +above +below v -above -below	1	0.05	0.8247
10	gap -below v +below	1	3.36	0.0712
11	gap +above v -above	1	0.23	0.6342
12	gap +above +below v -above -below	1	2.67	0.1068
13	sub -below v gap -below	1	1.57	0.2146
14	sub +below v gap +below	1	0.01	0.9162
15	sub -above v gap -above	1	1.50	0.2243
16	sub +above v gap +above	1	0.05	0.8205
17	natural shade v synthetic shade	1	0.00	0.9560
18	natural shade v no shade	1	0.00	0.9739
19	synthetic shade v no shade	1	0.00	0.9780

Table A3. Multiple contrasts for 1998 *N. leucotricha* vegetative tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.00526$) ** ($P < 0.05$ with Bonferroni correction $P < 0.00263$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.00053$).

	Contrast	**d.f.**	**F value**	**p**
	model	9	0.76	0.6568
1	subcanopy v gap	1	1.86	0.1773
2	+above v -above	1	0.19	0.6657
3	+below v -below	1	0.45	0.5032
4	+above +below v -above -below	1	0.45	0.5025
5	+above +below v -above +below	1	0.64	0.4257
6	+above -below v -above -below	1	0.04	0.8517
7	sub +below v -below	1	0.14	0.7140
8	sub +above v -above	1	0.18	0.6696
9	sub +above +below v -above -below	1	0.03	0.8659
10	gap -below v +below	1	0.38	0.5417
11	gap +above v -above	1	0.03	0.8619
12	gap +above +below v -above -below	1	0.10	0.7573
13	sub -below v gap -below	1	1.29	0.2602
14	sub +below v gap +below	1	0.63	0.4308
15	sub -above v gap -above	1	0.30	0.5874
16	sub +above v gap +above	1	1.59	0.2120
17	natural shade v synthetic shade	1	0.23	0.6344
18	natural shade v no shade	1	0.41	0.5231
19	synthetic shade v no shade	1	0.04	0.8412

Table A4. Multiple contrasts for 1998 *N. leucotricha* reproductive tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**p**
	model	9	0.99	0.4571
1	subcanopy v gap	1	2.14	0.1480
2	+above v -above	1	0.03	0.8545
3	+below v -below	1	0.64	0.4258
4	+above +below v -above -below	1	0.22	0.6389
5	+above +below v -above +below	1	0.13	0.7182
6	+above -below v -above -below	1	0.01	0.9190
7	sub +below v -below	1	0.01	0.9148
8	sub +above v -above	1	0.87	0.3532
9	sub +above +below v -above -below	1	0.60	0.4413
10	gap -below v +below	1	1.95	0.1665
11	gap +above v -above	1	0.17	0.6784
12	gap +above +below v -above -below	1	1.65	0.2037
13	sub -below v gap -below	1	3.42	0.0688
14	sub +below v gap +below	1	0.05	0.8261
15	sub -above v gap -above	1	2.86	0.0951
16	sub +above v gap +above	1	0.29	0.5921
17	natural shade v synthetic shade	1	2.19	0.1437
18	natural shade v no shade	1	0.72	0.3990
19	synthetic shade v no shade	1	0.60	0.4429

Table A5. Multiple contrasts for 1999 *N. leucotricha* shoot biomass ($g.m^{-2}$), tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**p**
	model	9	0.68	0.7203
1	subcanopy v gap	1	0.03	0.8607
2	+above v -above	1	1.23	0.2710
3	+below v -below	1	0.63	0.4316
4	+above +below v -above -below	1	0.06	0.8121
5	+above +below v -above +below	1	0.60	0.4413
6	+above -below v -above -below	1	0.63	0.4295
7	sub +below v -below	1	0.00	0.9533
8	sub +above v -above	1	0.57	0.4537
9	sub +above +below v -above -below	1	0.09	0.7705
10	gap -below v +below	1	1.39	0.2425
11	gap +above v -above	1	0.80	0.3742
12	gap +above +below v -above -below	1	0.04	0.8412
13	sub -below v gap -below	1	0.55	0.4594
14	sub +below v gap +below	1	0.24	0.6223
15	sub -above v gap -above	1	0.01	0.9194
16	sub +above v gap +above	1	0.16	0.6930
17	natural shade v synthetic shade	1	0.06	0.8145
18	natural shade v no shade	1	0.97	0.3285
19	synthetic shade v no shade	1	0.84	0.3624

Table A6. Multiple contrasts for 1999 *N. leucotricha* basal area change, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**p**
	Model	9	1.12	0.3602
1	subcanopy v gap	1	0.62	0.4350
2	+above v –above	1	0.09	0.7624
3	+below v –below	1	0.61	0.4384
4	+above +below v -above –below	1	1.01	0.3172
5	+above +below v -above +below	1	1.10	0.2974
6	+above -below v -above –below	1	2.19	0.1436
7	sub +below v –below	1	0.03	0.8591
8	sub +above v –above	1	0.04	0.8436
9	sub +above +below v -above –below	1	0.19	0.6654
10	gap -below v +below	1	2.10	0.1514
11	gap +above v –above	1	0.20	0.6583
12	gap +above +below v -above –below	1	1.79	0.1847
13	sub -below v gap –below	1	0.10	0.7508
14	sub +below v gap +below	1	2.04	0.1574
15	sub -above v gap –above	1	0.16	0.6911
16	sub +above v gap +above	1	0.60	0.4405
17	natural shade v synthetic shade	1	0.72	0.3999
18	natural shade v no shade	1	0.11	0.7360
19	synthetic shade v no shade	1	0.39	0.5354

Table A7. Multiple contrasts for 1999 *N. leucotricha* relative change in tillers/plant, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.00526$) ** ($P < 0.05$ with Bonferroni correction $P < 0.00263$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.00053$).

	Contrast	**d.f.**	**F value**	**p**
	Model	9	0.42	0.9227
1	subcanopy v gap	1	1.98	0.1638
2	+above v –above	1	0.05	0.8264
3	+below v –below	1	0.30	0.5885
4	+above +below v -above –below	1	0.35	0.5547
5	+above +below v -above +below	1	0.02	0.8805
6	+above -below v -above –below	1	0.21	0.6453
7	sub +below v –below	1	0.13	0.7208
8	sub +above v –above	1	0.09	0.7599
9	sub +above +below v -above –below	1	0.04	0.8406
10	gap -below v +below	1	0.18	0.6759
11	gap +above v –above	1	0.11	0.7408
12	gap +above +below v -above –below	1	0.28	0.5966
13	sub -below v gap –below	1	1.13	0.2908
14	sub +below v gap +below	1	0.86	0.3579
15	sub -above v gap –above	1	1.57	0.2149
16	sub +above v gap +above	1	0.57	0.4529
17	natural shade v synthetic shade	1	0.03	0.8641
18	natural shade v no shade	1	0.00	0.9606
19	synthetic shade v no shade	1	0.07	0.7871

Table A8. Multiple contrasts for 1999 *N. leucotricha* vegetative tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.00526) ** (P < 0.05 with Bonferroni correction P < 0.00263) and *** (P < 0.01 with Bonferroni correction P < 0.00053).

	Contrast	**d.f.**	**F value**	**p**
	Model	9	1.23	0.2938
1	subcanopy v gap	1	0.08	0.7767
2	+above v –above	1	0.01	0.9250
3	+below v –below	1	0.01	0.9391
4	+above +below v -above –below	1	0.07	0.7949
5	+above +below v -above +below	1	0.41	0.5255
6	+above -below v -above –below	1	0.60	0.4429
7	sub +below v –below	1	0.61	0.4388
8	sub +above v –above	1	0.74	0.3915
9	sub +above +below v -above –below	1	0.80	0.3749
10	gap -below v +below	1	1.16	0.2861
11	gap +above v –above	1	1.48	0.2283
12	gap +above +below v -above –below	1	2.62	0.1098
13	sub -below v gap –below	1	0.54	0.4644
14	sub +below v gap +below	1	1.30	0.2589
15	sub -above v gap –above	1	0.85	0.3599
16	sub +above v gap +above	1	1.44	0.2337
17	natural shade v synthetic shade	1	3.28	0.0745
18	natural shade v no shade	1	1.29	0.2596
19	synthetic shade v no shade	1	0.68	0.4120

Table A9. Multiple contrasts for 1998 *B. dactyloides* plant density change, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	1.73	0.1662
1	subcanopy v gap	1	0.59	0.4460
2	+above v –above	1	5.47	0.0252
8	sub +above v –above	1	1.41	0.2436
11	gap +above v –above	1	4.22	0.0475
15	subcanopy -above v gap –above	1	0.71	0.4068
16	subcanopy +above v gap +above	1	0.05	0.8303
17	natural shade v synthetic shade	1	0.37	0.5459
18	natural shade v no shade	1	4.62	0.0386
19	synthetic shade v no shade	1	3.56	0.0677

Table A10. Multiple contrasts for 1998 *B. dactyloides* relative change in tillers/plant, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	1.71	0.1691
1	subcanopy v gap	1	0.64	0.4309
2	+above v –above	1	0.01	0.9066
8	sub +above v –above	1	2.23	0.1442
11	gap +above v –above	1	2.90	0.0976
15	subcanopy -above v gap –above	1	4.96	0.0324
16	subcanopy +above v gap +above	1	0.79	0.3814
17	natural shade v synthetic shade	1	0.21	0.6474
18	natural shade v no shade	1	0.16	0.6948
19	synthetic shade v no shade	1	0.01	0.9363

Table A11. Multiple contrasts for 1998 *B. dactyloides* tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	0.31	0.8683
1	subcanopy v gap	1	0.13	0.7186
2	+above v –above	1	0.01	0.9157
8	sub +above v –above	1	0.29	0.5947
11	gap +above v –above	1	0.77	0.3853
15	subcanopy -above v gap –above	1	0.27	0.6097
16	subcanopy +above v gap +above	1	0.92	0.3450
17	natural shade v synthetic shade	1	0.46	0.5024
18	natural shade v no shade	1	0.14	0.7119
19	synthetic shade v no shade	1	0.14	0.7106

Table A12. Multiple contrasts for 1998 *B. dactyloides* reproductive tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	1.19	0.3336
1	subcanopy v gap	1	1.96	0.1701
2	+above v –above	1	1.72	0.1985
8	sub +above v –above	1	2.43	0.1284
11	gap +above v –above	1	0.35	0.5566
15	subcanopy -above v gap –above	1	2.27	0.1409
16	subcanopy +above v gap +above	1	0.75	0.3915
17	natural shade v synthetic shade	1	0.26	0.6142
18	natural shade v no shade	1	0.41	0.5278
19	synthetic shade v no shade	1	1.97	0.1691

Table A13. Multiple contrasts for 1999 short-grass ANPP, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.011$) ** ($P < 0.05$ with Bonferroni correction $P < 0.0055$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.0011$).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	1.28	0.2956
1	subcanopy v gap	1	3.32	0.0770
2	+above v –above	1	0.56	0.4576
8	sub +above v –above	1	0.01	0.9427
11	gap +above v –above	1	0.60	0.4425
15	subcanopy -above v gap –above	1	2.58	0.1172
16	subcanopy +above v gap +above	1	0.78	0.3818
17	natural shade v synthetic shade	1	0.26	0.6161
18	natural shade v no shade	1	0.05	0.8251
19	synthetic shade v no shade	1	0.80	0.3783

Table A14. Multiple contrasts for 1999 *B. dactyloides* plant density change, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	1.76	0.1590
1	subcanopy v gap	1	1.87	0.1810
2	+above v –above	1	0.35	0.5594
8	sub +above v –above	1	0.37	0.5480
11	gap +above v –above	1	0.02	0.8765
15	subcanopy -above v gap –above	1	0.18	0.6700
16	subcanopy +above v gap +above	1	1.77	0.1925
17	natural shade v synthetic shade	1	6.28	0.0172
18	natural shade v no shade	1	4.39	0.0438
19	synthetic shade v no shade	1	0.22	0.6448

Table A15. Multiple contrasts for 1998 *B. dactyloides* relative change in tillers/plant, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * (P < 0.1 with Bonferroni correction P < 0.011) ** (P < 0.05 with Bonferroni correction P < 0.0055) and *** (P < 0.01 with Bonferroni correction P < 0.0011).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	2.08	0.1042
1	subcanopy v gap	1	2.31	0.1372
2	+above v –above	1	1.51	0.2280
8	sub +above v –above	1	5.22	0.0285
11	gap +above v –above	1	0.12	0.7328
15	subcanopy -above v gap –above	1	6.11	0.0184
16	subcanopy +above v gap +above	1	0.03	0.8632
17	natural shade v synthetic shade	1	0.64	0.4296
18	natural shade v no shade	1	0.15	0.7049
19	synthetic shade v no shade	1	2.09	0.1570

Table A16. Multiple contrasts for 1999 *B. dactyloides* reproductive tiller density, tree-grass competition treatments. Positive (+) and negative (-) sign refers to presence or absence of competition. Significant effects are indicated by * ($P < 0.1$ with Bonferroni correction $P < 0.011$) ** ($P < 0.05$ with Bonferroni correction $P < 0.0055$) and *** ($P < 0.01$ with Bonferroni correction $P < 0.0011$).

	Contrast	**d.f.**	**F value**	**p**
	Model	4	0.79	0.5387
1	subcanopy v gap	1	2.75	0.1061
2	+above v –above	1	0.48	0.4939
8	sub +above v –above	1	0.00	0.9992
11	gap +above v –above	1	0.41	0.5238
15	subcanopy -above v gap –above	1	1.94	0.1723
16	subcanopy +above v gap +above	1	0.75	0.3934
17	natural shade v synthetic shade	1	0.19	0.6676
18	natural shade v no shade	1	0.65	0.4268
19	synthetic shade v no shade	1	0.21	0.6524

VITA

Mark Trevor Simmons

Born: 30th April 1960. Nottingham, U.K.

Education:

1981 B.Sc. (Environmental Science),
University of Lancaster, U.K.

1992 B.Sc. (Botany),
University of Cape Town, South Africa

1993 B.Sc. (Hons) (Botany),
University of Cape Town, South Africa

1997 M.Sc. (Botany),
University of Cape Town, South Africa

2003 Ph.D. (Rangeland Ecology and Management)
Texas A&M University, College Station, Texas, U.S.A.

Address:

14424 Evergreen Cove
Austin
Texas
U.S.A.